Conserving Native Pollinators

A literature review considering the appropriate use of buffers around Colorado rare plants

Phacelia formosula, by Peter Gordon

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Executive Summary

The conservation of rare plants is a challenging and ever evolving task. As almost 90% of the world's flora depends on animal pollinators for reproduction, it is critical that these pollinators are accounted for in conservation strategies. This document summarizes a literature review conducted by the BLM which attempts to address the best way to conserve these pollinators, and presents a novel solution endorsed by the BLM Colorado State Botanist (Carol Dawson).

We begin by presenting a list of 15 rare plant species which occur on BLM land within Colorado and summarize all known insect visitors to each plant. In reviewing how these data have been used by the Fish and Wildlife Service (FWS) to create buffer distances (protected areas around the occupied habitat of the rare plants), we point out several concerns with their methods. Our concerns include limitations in both the available pollinator data and in the equations which have been used to determine foraging distances of these pollinators.

After conducting an extensive literature review on the foraging behaviors of both social and solitary bee species, we suggest that a 500 meter buffer is appropriate around all bee-pollinated rare plants in Colorado. We feel that this is a reasonable distance that will protect the entire pollinator community, rather than only those species which have been observed visiting each plant.

Our literature review suggests that the majority of solitary bees forage within such an area naturally, meaning that their nests sites are likely to be protected. Social bees often forage at great distances from their nests (up to several kilometers), and are willing to cross inhospitable habitat in order to reach their forage. Thus, even if some social bees nest outside of our buffers, the protection of such large tracts of land ought to provide sufficient foraging opportunities to attract these social species. Together, these observations validate the recommendation of the State Botanist that a 500 meter buffer be implemented around Colorado rare plants.

Introduction

The Bureau of Land Management (BLM) manages 8.3 million acres of land in the state of Colorado on which at least 75 rare plant species grow. These rare plants have either been formally listed under the Endangered Species Act or identified by the BLM State Director as Sensitive Species. The BLM must develop and implement appropriate conservation measures in the management of Bureau special status species and the ecosystems upon which they depend. Recently, conservationists have begun to pay a lot of attention to how rare plants interact with their pollinators, as approximately 87% of the world's flora depends on animal pollinators for reproduction and the maintenance of genetic viability (Ollerton *et al.* 2011). Thus, it is paramount that pollinators be taken into account when designing conservation measures for rare plants. This document discusses how the Bureau (and other land managers) can best consider native pollinators while protecting the rare plants that fall within their purview.

Of particular concern to land managers is how far pollinators (in our case represented primarily by native bees) fly. Pollination is likely to suffer if plant populations are separated by a distance greater than pollinators fly, or alternately, if a pollinator's nesting biology is not taken into account (Cane 2001). Different bee species have a wide variety of nesting requirements, and often the resources required for nesting are spatially separated from the flowers that the bees forage at and pollinate (Westrich 1996, Cane 2001). Thus, simply protecting occupied habitat is not enough to guarantee persistence of our rare plants, we must also provide appropriate nesting habitat within the pollinator's flight range. As it is extraordinarily difficult to locate native bee nests in the field (Dramstad 1996, Darvill *et al.* 2004, Goulson 2010), land managers are accounting for nesting requirements by creating protective buffers around occupied habitat.

The Fish and Wildlife Service (FWS) has produced a draft Guidance for Section 7 Consultations that Include Plants within the State of Colorado document that incorporates plant species-specific potential buffer distances (FWS calls them "plant consideration zones," or sometimes "plant set-back distances"). These areas are used to calculate whether surveys and/or consultation needs to occur under Section 7. The widths of the buffers vary by plant species, and have been created based on what is known or inferred about the foraging distance of the pollinators known to visit each specific plant. To date, these numbers are primarily based on one key paper (Greenleaf *et al.* 2007), which predicts bee flight distances based on body size. The proposed buffer distances range from 100 m (*Phacelia submutica*) to 1000 m (*Penstemon debilis* and *P. penlandii*, as well as 3 other species that are not focus plant species of this review), and are summarized in Table 1.

The document that follows provides a summary and an interpretation of an in-depth literature review conducted by the BLM that sought to broaden our knowledge regarding the foraging distances of native pollinators. Upon completion of the literature review we (with the endorsement of the BLM Colorado State Botanist, Carol Dawson) propose a single buffer distance of 500 meters for all Colorado rare plants that depend on native bees for pollination.

The plants & their pollinators

The plants

The BLM has compiled a list of 15 rare Colorado plant species ("focus plant species") that exist on land managed by the Bureau (see Table 1). These plants provide a lens through which to look at appropriate buffer distances. All but one of the species have been recognized under the Endangered Species Act (either as a candidate, proposed, threatened, or endangered species) and 3 of the 15 have been designated BLM Sensitive Species. These rare plant species reflect a diverse array of taxa, representing 8 genera in 7 families. They grow in many different habitats, from deserts to shrub-steppe communities to high alpine environments.

The visitors

These plants are visited by a diverse assemblage of native insects; including bees, wasps, ants, flies, butterflies, and even a beetle. Despite this diversity, across the plant taxa the majority of the described visitors are solitary bees (Fig. 1). Bumblebees also appear to play an important role for several of the plant species, and while non-bee visitors are prevalent for a few of the species, generally they are not common. Honeybees have only been observed visiting 3 of our focus plants. Due to these patterns of observed visitor compositions, this review focuses entirely on native bees (both solitary and social). Because ants are believed to play a large role in the pollination of *Eriogonum pelinophilum* (Bowlin *et al.* 1992) and *Phacelia submutica* is believed to be self-pollinated (Service 2011a, Clark 2012), both deserve further study and the recommendations from this review should not be applied without additional species-specific knowledge.

The bees

Estimates suggest that there may be as many as 20,000 species of bees worldwide, approximately 3,500 of which are found in North America above Mexico (Michener 2007, Mader *et al.* 2011). A recent synthesis listed 946 extant bee species in Colorado, and even this is believed to be an underestimate as not all parts of the state have been thoroughly surveyed (Scott *et al.* 2011). While much of agriculture is now dependent on introduced and managed honeybee hives for pollination, native plants have traditionally relied on native bees, and it seems that this is still the case for our focus plant species. Indeed, there is evidence that honeybees are less effective pollinators of many plants (Winfree 2010) and that they compete for resources with native bees in the areas in which they coexist (Thomson 2004). Thus, counting on honeybees to provide effective pollination services for our rare plants is neither likely to work nor ecologically responsible. Instead, we must focus on protecting native pollinator communities.

Bees are some of the most effective pollinators because they are lifelong obligate florivores, actively gathering pollen to feed their young and nectar to feed themselves. While other insects often visit flowers to collect nectar, any pollen they transfer is accidental. As active foragers, bees can be broadly split into three strategic groups. Polylectic bees are generalists, visiting a variety of plant species, while oligolectic species specialize on a limited number of taxa. Cleptoparasitic bees are parasites which lay their eggs in brood cells that have already been created and provisioned by other bees. Thus, they do not actively forage for pollen, and tend to be much less important as pollinators.

Bees exhibit a wide diversity of life history traits. A primary division can be drawn between social and solitary species. Honeybees and bumblebees are social, creating large colonies run by a single queen. These colonies tend to be present throughout the season, which means that the species that live in them are usually generalists, forced as they are to forage on a temporally changing diversity of floral resources. In return, the social bees provide pollination services to many different plants. Solitary species are far more common, accounting for c. 90% of all described bee species (Mader *et al.* 2011). Each solitary female creates a nest for her own young. During her short adult life (generally 3-6 weeks [Mader *et al.* 2011]), she gathers pollen to provision brood cells in which she lays her eggs. Because only one bee is flying in and out of these nests, they are extraordinarily difficult to locate. Many solitary bees are also generalists, though due to their generally short lifespan some species are able to be specialists.

However, it is misleading to divide social and solitary bees so neatly. Some bees (which I have grouped with the solitary bees in this document for simplicity's sake) fall somewhere in the middle of the sociality spectrum. Without forming traditional colonies, these species may nest communally, sharing an area or even a nest entrance with several to hundreds of individuals. However, within this common space each female creates her own nest and provisions her own brood cells for her young. Thus, their foraging behaviors are much more similar to those of the solitary bees than to those of the social species.

Different bee species exhibit different nesting behaviors (Cane 1991). Many are ground-nesters, either creating their own burrows or using existing holes dug out by rodents or other small animals. Some bumblebee species nest aboveground, especially in grassy tussocks. Some solitary bees nest in pithy stems, and others nest in pre-existing cavities in wood, rocks, or even snail shells. While it is tempting to attempt to manage habitats for specific nesting materials, this diversity in nesting preferences and a lack of species-specific nesting data makes it very difficult. Instead, if the bees are currently present and pollinating our plants than it means that they must have sufficient nesting habitat already. By placing a buffer around the habitat occupied by the plant we ought to be protecting enough nesting habitat to sustain the bee populations as well, especially if the buffer encompasses the typical foraging distance of a species.

Taken together, these varied life history traits help explain the difficulties involved in creating buffer distances based on a pollinator's foraging distance, as many different factors are likely to influence how far a bee forages from its nest. This diversity will be discussed throughout this review.

A note on data

While Figure 1 summarizes all recorded visitors to each of the 15 focus plant species, the available pollinator data vary widely in quality and completeness. Some species have been heavily studied and many potential pollinators have been described, while others have never even been studied. For example, 54 species have been observed visiting *Penstemon debilis* (McMullen 1998), while I was unable to find any records that looked for insect visitors to *Eutrema penlandii* or *Penstemon harringtonii*. What's more, different pollinator studies follow various methodologies and overall sampling effort is unequal between plant species. Thus, while the total numbers of species that have been observed visiting a plant are represented in both Table 1 and Figure 1, it is unlikely that any of these numbers represent the true number of insect pollinators. On one hand, further sampling and studies will probably reveal more visitors as more effort is expended looking for them, especially because pollinator species composition often changes between years (Petanidou *et al.* 2008). On the other hand, we must remember that not all visitors are pollinators (Kwak *et al.* 1998, Forup & Memmott 2005), and that these numbers may overestimate the number of species that are ecologically important. At present, however, these data are what have been used to create the proposed buffer distances by the FWS.

Why the status quo is insufficient

Species composition

The primary issue with using the proposed buffer distances is that they are based on supposed foraging distances of specific pollinators. As discussed above, our knowledge of which pollinators are important for each plant is limited. The majority of the studies which have been conducted did not distinguish between insect visitors and insect pollinators, an important oversight as visitation does not guarantee or even adequately predict pollination (Kwak *et al.* 1998, Forup & Memmott 2005). Further, there is good evidence that plant-pollinator communities and their interactions are highly variable over time (Price *et al.* 2005, Petanidou *et al.* 2008) and that often the important pollinators will change between years (Burkle & Alarcon 2011). Several pollinator studies demonstrate this theory, finding that only 20% of all pollinators in a study site were present all four years of the study (Petanidou *et al.* 2008) and that only 25% of pollinator-plant interactions observed in one year were present in the next (Dupont *et al.* 2009). Even the authors of the study reporting the insect visitors of *Spiranthes diluvialis* (one of our focus plants) after the third year of observations noted that the species composition was significantly different from what had been reported after the first two years (Pierson *et al.* 2000).

Together, these studies suggest that we can’t make conclusive statements about the required pollinators for each specific plant based on only a few years of data. Unfortunately, this is the amount of data that is often available. For 11 of the 13 focus species for which insect visitors have been observed, the pollinator observations have occurred over the course of only one or two years (Karron 1987, Heil & Porter 1990, Warren 1990, McMullen 1998, Rechel *et al.* 1999, Tepedino *et al.* 1999, Lewinsohn & Tepedino 2004, Lewinsohn *et al.* 2005, Tepedino 2009, Tepedino *et al.* 2011). Visitation data were collected over the course of three seasons for the remaining two species (*Penstemon grahamii*: Lewinsohn & Tepedino 2004, Lewinsohn *et al.* 2005, Tepedino 2008; *Spiranthes diluvialis*: Sipes & Tepedino 1995, Pierson *et al.* 2000). While these data are certainly interesting and useful to have, neither two nor three years of study is enough to be even relatively certain of the important pollinators. Thus, it is difficult to justify using such limited data to devise conservation strategies.

Network resiliency

Luckily, it doesn’t seem that we need to know all of the specific plant-pollinator interactions that occur, nor do we need to worry about year-to-year shifts in pollinator composition. Pollination networks are resilient to such natural changes, incorporating both species redundancy and a nested structure

(Bascompte *et al.* 2003, Memmot *et al.* 2004, Olesen *et al.* 2008, Burkle & Alarcon 2011). Redundancy refers to the fact that the majority of species are generalists (the proportion of specialists is likely to have been overestimated in the past [Petanidou *et al.* 2008]), and thus not dependent on a single partner species for persistence. Therefore, even if a pollinator is lost from a network its function can usually be replaced by another pollinator, especially if the plant species affected is a generalist. There is no evidence that any of our focus plants depend on a single pollinator species or genus for reproduction, meaning that they can take advantage of this resiliency.

The nestedness of a network categorizes how connected the various species involved in mutualistic interactions are. In a highly nested network the more specialist species interact with a proper subset of the more generalist partners (Bascompte *et al.* 2003). In other words, a highly nested network is characterized by asymmetrical specialization, in which a specialist bee may pollinate a generalist flower, or a specialist flower may be pollinated by a generalist bee. Asymmetrical specialization is resilient because it means that the extinction of a specialist is unlikely to result in its partner's extinction. This pattern seems to be much more common than the traditionally accepted theory that the majority of specialist pollinators and specialist flowers evolved together (Bascompte *et al.* 2003, Memmott *et al.* 2004). A nested, redundant network can easily deal with some changes in species composition, and due to the abundance of such networks it seems quite likely that our rare plants are components in just such a network. Therefore, they too should be quite resilient; not only to natural year-to-year variation, but also to slight changes brought about by development.

This resiliency has been documented and discussed in several studies. Petanidou *et al.* (2008) state that "it is very likely that the great majority of both plants and pollinators will find new interaction partners if their present partners vanish." Memmott *et al.* (2004) modeled species loss in pollinator communities, and found that if the most specialized pollinators were removed first (ecologically likely as they tend to be rarer and seem to be more susceptible to extinction) plant species went extinct very slowly in response until the vast majority of pollinators were lost. Even if more highly-linked species were lost first, the overall decline in plant diversity was no worse than linear (Memmott *et al.* 2004). This exercise demonstrated that the extreme "extinction vortexes" that have been predicted elsewhere are unlikely to occur due to pollinator loss. Moreover, even in restored ecosystems where the pollinator community has changed significantly, the new community has been shown to maintain pollination services (Forup & Memmott 2005, Williams 2011). These studies suggest that our focus plants should be able to sustain the loss of some of their current pollinators, as the networks in which they exist ought to provide alternative pollinators that will be able to functionally replace those that are lost.

Conserving the pollinator community

None of the above is meant to imply that we can ignore pollinators while designing conservation strategies. With extreme fragmentation, all pollinator communities are likely to be lost, and no amount of resiliency can prevent this. Instead, the above argument is presented in order to demonstrate that creating buffer distances based on a small number of known insect visitors is not a responsible decision. Rather, we should attempt to conserve an entire healthy pollinator community, even if we don't know which species may make up the community. Maintaining species diversity is more important than maintaining the individual species that are present at any one time, as the majority of plants depend on a diverse community of pollinators (Slagle & Hendrix 2009, Williams 2011). Because we have so little knowledge about what bee species may make up the various communities in each ecosystem, we advocate attempting to preserve as many species as possible in each location. The easiest way to do this is to create a single buffer distance that applies across ecosystems, though determining an appropriate width for this buffer is, of course, challenging.

Issues with the equations currently used

So far, foraging distances of North American bees as they relate to the conservation of Colorado rare plants have been estimated primarily from a few key papers (Gathmann & Tscharntke 2002, Greenleaf *et al.* 2007). These papers each present equations that predict a species' maximum flight distance based on body size, either length (Gathmann & Tscharntke 2002) or intertegular span (the length between the wing tegulae; Greenleaf *et al.* 2007). Because bumblebees are the largest bee species in our ecosystems, any plant species for which bumblebee visitors have been observed has been given a buffer distance of 1000 m (Table 1). For plants which seem to be visited only by smaller bees (i.e. *Osmia*), buffer distances are as low as 400 m. Beyond the issues discussed above regarding the use of observed visitors to create buffers, there are several problems related to using these specific papers as our sole predictor of foraging distance. Primarily, while the equations are relatively robust (especially in Greenleaf *et al.* 2007), they are developed using a limited number of bee species. *None* of the species used are known pollinators of our rare plants, and the vast majority are not even found in North America.

The species used also encompass many different bee families. This choice by Greenleaf *et al.* (2007) allows their equations to be applied to any and all bee species. However, it ignores the vast variability in sociality, life history, foraging behaviors, and nesting habits that are also likely to play a role in species-specific foraging distances. Species that nest in large colonies, such as bumblebees, should logically utilize a greater area in order to provision the entire nest (Goulson 2010) than solitary bees need if only provisioning a couple dozen brood cells. This trend can be hidden if all species are grouped together, as bumblebees also tend to be larger than solitary bees. Oligolectic (specialist) bees can be expected to travel further than generalists if the forage on which they're specialized grows in a patchy distribution (e.g. Zurbuchen *et al.* 2010a). Bees that are present throughout the entire season, or which have more than one generation per year, may at times need to travel long distances in order to reach seasonally available forage (Roulston & Goodell 2011). Finally, bees are likely to display adaptations and thus forage distances that are specific to their habitat. The distribution of plants in a desert is dramatically different from the distribution of plants in the tropics, which is again different from within a temperate forest. These variations in bee ecologies highlight some factors other than body size which probably contribute to foraging distances. We must consider functional groups separately in order to take these differences into account before developing conservation recommendations based on foraging distances.

The third problem with using the equation from Greenleaf *et al.* (2007) is that it is calculated to predict maximum flight distance, and doesn't necessarily tell us much at all about actual foraging distance. In this context, "flight distance" means the maximum distance that an individual or species is physically capable of flying, while "foraging distance" refers to how far these species generally travel while actively foraging. Because of these fundamental differences, manipulative (i.e. experimental) study designs generally test maximum flight distances, while observational studies are better for measuring foraging distances. However, this distinction illustrates the difficulty faced by researchers who study these topics. It is far easier to experimentally measure the distance an individual can physically fly than it is to design an observational study that sheds light on the greatest foraging distance traveled, especially as foraging distance varies by individual (Zurbuchen *et al.* 2010c), by resource availability in the specific habitat (Darvill *et al.* 2004, Wolf & Moritz 2008), and by season (Osborne *et al.* 1999, Knight *et al.* 2005, Wolf & Moritz 2008, Elliott 2009). In any case, even if one were able to determine a maximum foraging distance for a specific bee species, there is growing acceptance that the maximum foraging distance is not nearly as important for conservation as the mean foraging distance (Zurbuchen *et al.* 2010c).

The flight distance studies used by Greenleaf *et al.* (2007) to create their equations fall into two categories. The first are homing experiments, in which bees are displaced various distances from their nest and the rate of return is calculated from each distance. The furthest distance from which 10% of individuals return is assumed to be the maximum flight distance. Greenleaf *et al.* also used these studies to calculate a "typical" flight distance, from which 50% of individuals returned (Williams, personal communication *in* Tepedino 2009, corrects misstatements from the original Greenleaf *et al.* 2007 paper). Even if the equation they created works perfectly to determine how far a bee is capable of flying, multiple inferences must be made to link these flight distance data to an average foraging distance for the species (Knight *et al.* 2005, Westphal *et al.* 2006), a fact which Greenleaf *et al.* concede.

The second method used is a feeder-training method, in which plant/feeder patches are placed at various distances from the nest and the number of bees that forage at the patch at each distance is observed. While this is a more applicable study design, it is generally limited to use with oligolectic bees and, as discussed above, oligolectic species may be expected to fly further than generalists of the same size. Overall it is difficult to accept that these equations will perfectly predict foraging distances of the bees which we are interested in, and once we take varying species composition into account they become almost impossible to trust to create meaningful buffers.

Our strategy

This section has discussed some of the difficulties involved in creating plant species specific buffers. Pollinator composition for each plant species is often not known or poorly documented, and compounding this issue, composition is variable across time and space. However, plant-pollinator communities are resilient to this variation due to built-in redundancy and a nested structure. Thus, conservation recommendations should focus on the entire community, not simply the few potential pollinators that may have been observed during a year or two of study. Determining foraging distances of individual pollinators is also problematic, as the equations used to date are built from studies that test flight distance rather than foraging distance and are based on a limited number of species. Further, those species are all lumped together into one equation that doesn't take variability in life histories into account.

By studying the major functional groups of pollinating bees separately and then pulling the resulting information together into a single proposed buffer distance, we hope to overcome these difficulties. We believe that we have come to a solid scientific recommendation that will hopefully protect the entire community. By using one inclusive buffer distance we will avoid protecting only a small subset of the entire pollinator community (as this may be all that has been observed to date) while also creating a single conservation strategy which will be easier to implement and explain to stakeholders. In the rest of this document we will first discuss the buffer distances required by bumblebees and other social bees and then consider those required by solitary bees before drawing the two groups together.

Bumblebees

Introduction

Pollinator guilds are generally dominated by solitary bees, while bumblebees tend to play a secondary role (see Fig. 1). However, bumblebees are the largest of our native pollinators, providing the driving force behind the widest buffers suggested by FWS (1000 m). They have also been much more thoroughly studied than solitary bees, making them a good group to discuss first.

Bumblebees all belong to the genus *Bombus* in the family Apidae, and nest in large colonies that tend to be present from spring until fall. Because these colonies persist for so long, bumblebees take advantage of many different floral resources throughout the season (they're generalists). Due to their large colonies and generalist foraging strategies, they can be expected to forage great distances from their nests. While the literature currently supports this expectation, it took some time to get to this point.

History of thought

Bombus foraging strategies are a complex and poorly understood topic. Bumblebees are big bees, and so are expected to have the ability to fly long distances (e.g. Gathmann & Tscharntke 2002, Greenleaf *et al.* 2007). Until recently, however, researchers assumed that they would choose to forage near their nests if resources were readily available to maximize energy efficiency (reviewed in Goulson 2010). The results of several mark-recapture studies conducted on bees caught while foraging reinforced this theory, reporting flight distances of only a few hundred meters (see, e.g., Bowers 1985, Bhattacharya *et al.* 2003, Elliott 2009). Despite the fact that nest location was unknown, researchers assumed that because the bees were caught repeatedly within a small area they probably nested nearby. Several early studies that marked bumblebees at the nest built this assumption into their methods, sampling only within a few hundred meters of the nest. Researchers reported low foraging distances based on the small percentage of bees that were recaptured, while explaining away the disappearance of many bees.

Dramstad (1996) reviewed these papers and suggested that the "missing" bees were simply foraging outside of the heavily sampled area in which the researchers expected to find them, then backed this hypothesis up with data of her own. She demonstrated a high recapture rate of bumblebees marked while foraging inside her study meadows, but extremely low recapture rates of those bees marked at nests placed at the edge of the same meadow. The bees, she concluded, returned repeatedly to favored forage sites (site constancy) but the location of that forage was not necessarily near the location of the nests, and in fact, it was likely to be some distance away. Her paper has been cited 76 times since its publication, reflecting a general shift in the understanding of bumblebee foraging patterns as more scientists come to accept this explanation (e.g. Saville *et al.* 1997, Cresswell *et al.* 2000, Walther-Hellwig & Frankl 2000, Chapman *et al.* 2003, Darvill *et al.* 2004, Knight *et al.* 2005, Osborne *et al.* 2008).

Bumblebee specific problems with the current equations

Beyond the fact that the equations currently in use are based on maximum flight distances gathered from homing experiments and group together many different taxa (see discussion in “Issues with the equations currently used”), they are not even appropriate for predicting bumblebee flight distances. Gathmann and Tscharntke (2002) based their models solely on solitary bee species, making them unfit to model bumblebee flight distances at all. Greenleaf *et al.* (2007), on the other hand, included one data point gathered from *Bombus terrestris*, a European bumblebee. The remainder of their input data came from solitary bees and honeybees. A single data point from a bumblebee is simply not enough to convincingly demonstrate that this equation will work for the *Bombus* species that we are concerned about.

Alternative methods to determine foraging distance

So if we can’t predict bumblebee foraging distances from equations based on body size or from homing experiments, how can we determine the scale at which the bees forage? Observational techniques, while generally unable to tell us anything about maximum flight distance, are much more reliable for learning about the true ecology of a species. By observing bees in the field, researchers can determine how far a bee actually travels on a day-to-day basis, rather than how far it is capable of travelling when forced to. There are several observational techniques that have been used to quantify *Bombus* foraging distances.

One of these methods is measuring the genetic relatedness of foraging bumblebees. This works because all foragers within a colony are sisters, and thus if two sisters are found at a distance of 300 m from each other it can be assumed that they each traveled at least 150 m from the nest. Studies utilizing this method have returned a wide range of foraging distances. *Bombus terrestris* was found to have a median foraging distance of 0.62-2.8 km (max foraging distance 0.87-3.9 km) in one study (Chapman *et al.* 2003), a max distance of up to 758 m in another (Knight *et al.* 2005), and a maximum of 625 m in a third (Darvill *et al.* 2004). *Bombus pascuorum* had a similarly wide range reported in these studies, from a max foraging distance of 0.72-3.2 km (Chapman *et al.* 2003), to 449 m (Knight *et al.* 2005), to staying within 312 m (Darvill *et al.* 2004). Knight *et al.* (2005) also looked at *B. lapidarius* (max foraging distance 450 m) and *B. pratorum* (max distance 674 m). While this method is observational, it also has built in assumptions related to nest density. Further, as it returns such a wide range of numbers, it clearly does not lead to an easy conclusion about a species’ average foraging distance.

A popular method to estimate foraging ranges is to mark bees at the nest and attempt to recapture them while foraging. This method has its own built in assumptions and issues and also returns a wide range of bumblebee foraging distances, from <100 m to 2.2 km (see Dramstad 1996, Saville *et al.* 1997, Walther-Hellwig & Frankl 2000, Dramstad *et al.* 2003, Kreyer *et al.* 2004, Wolf & Moritz 2008). A related technique is to attach harmonic radar transponders to bees as they leave the nest, then to track their movements. Osborne *et al.* (1999) used this technology to observe bumblebee behaviors, but were limited in their conclusions because the transponders only worked up to 700 m from the radar dish, and only if the bee remained within a clear line of sight.

Westphal *et al.* (2006) examined the spatial scale at which different bumblebee species utilized resources in order to estimate foraging distances. They returned large resource use areas which varied greatly by species, from circles with a 250 m diameter for *B. pratorum* to a 3,000 m diameter for *B. terrestris*. When

Goulson (2010) reviews this study, he suggests dividing the numbers in half in order to gain a better estimate of foraging distance, as nests are likely to occur in the center of these resource use circles. Thus, foraging distances range from 125 m to 1,500 m (Goulson 2010). Overall, Wolf and Moritz (2008) summarize the state of our knowledge quite well, declaring that "estimates of foraging ranges have one aspect in common: they are highly variable."

The forage landscape

These studies do succeed in demonstrating that bumblebees as a genus don't seem to be "doorstep foragers," only selecting forage that is near their nest (though some rare, specialized species appear to be the exception [see Walther-Hellwig & Frankl 2000]). Instead, many of the authors report that bumblebees will fly over seemingly acceptable forage in order to get to a different patch (Dramstad 1996, Saville *et al.* 1997, Osborne *et al.* 1999, Walther-Hellwig & Frankl 2000, Dramstad *et al.* 2003, Osborne *et al.* 2008). The reason they do this ultimately seems to come down to patch quality.

Cresswell *et al.* (2000) present an economic flight model that suggests bumblebees could beneficially fly up to 10 km to reach a patch of particularly rewarding forage, while Wolf and Moritz (2008) were able to explain 80% of forage distance variation by distance from the nest and forage quality. Bumblebees are fast fliers (Riley *et al.* 1999), so not much time is wasted travelling to a distant site. If the energy expended flying to a distant site can be compensated for by the increased rewards found there, it will be economically viable for a bumblebee to make that flight (Cresswell *et al.* 2000). Also, bumblebees are known to exhibit site constancy (Osborne & Williams 2001), so once they have found a great forage patch they are likely to return to it over and over again, explaining the short flight distances found by studies that mark bees while foraging (e.g. Bowers 1985, Bhattacharya *et al.* 2003, Elliott 2009).

Relating these data to our pollinators

As discussed above, foraging estimates vary remarkably between species, with very little consensus. Further complicating this matter, to date every single bumblebee species for which flight range has been calculated is European (Dramstad 1996, Saville *et al.* 1997, Walther-Hellwig & Frankl 2000, Chapman *et al.* 2003, Dramstad *et al.* 2003, Darvill *et al.* 2004, Kreyer *et al.* 2004, Knight *et al.* 2005, Wolf & Moritz 2008). There is next to no data available regarding foraging range of North American bumblebees, and that which does exist tends to have marked the bees while foraging (Bowers 1985, Elliott 2009).

So, with the data limitations that currently exist, is it even possible to make conclusions about the foraging distances of the bumblebees that we're interested in? Despite the wide variation in recorded flight distances, there are interspecific trends that emerge (Fig. 2) when one compares the five studies which have provided foraging distance estimates for more than one species (Walther-Hellwig & Frankl 2000, Chapman *et al.* 2003, Darvill *et al.* 2004, Knight *et al.* 2005, and Westphal *et al.* 2006). *Bombus terrestris* generally had a longer foraging range than any other bumblebee it was studied with. Walther-Hellwig and Frankl, Chapman *et al.*, Darvill *et al.*, and Westphal *et al.* all found a positive correlation (though none calculated it statistically) between foraging distance and body size, in that the larger bees foraged greater distances. However, Knight *et al.* found that *B. pratorum*, the smallest observed bee, had the second greatest foraging distance. They suggested instead that foraging distance could be related to colony size, though they didn't quantify colony size, and it appears that *B. pratorum* makes small colonies anyway. Despite this incongruence, there seems to be a growing acceptance that foraging distance is related to colony size (see Goulson 2010). The bigger the colony, the reasoning goes, the larger a foraging area would need to be in order to supply enough food and avoid intraspecific competition (Knight *et al.* 2005). While this makes sense, it is interesting that Goulson (2010) accepts it as the only predictor of foraging distance without mentioning that for all bees studied body size decreases with decreasing colony size. Thus, it is difficult to separate these two factors, and indeed both may contribute to a species' average foraging distance. Unfortunately, neither factor has a clear linear relationship with foraging distance that we would be able to apply to our bumblebees (Fig. 2).

Conservation recommendations

There is good evidence that many bumblebees are able to fly further than a kilometer to forage. Taking this into account, how can we responsibly provide for their protection and continued presence as pollinators of our native rare plants without fencing off miles and miles around the entire habitat? Bumblebee nests are notoriously difficult to find in the field, even by experts (Dramstad 1996, Darvill *et al.* 2004, Goulson 2010), and the area in which they may occur is enormous (assuming a bumblebee flight distance of 1 km would give 776 acres of potential nest sites) and so it seems infeasible to survey for nests during preliminary site surveys. Without knowing where the nests occur, how can we protect the bees?

While bumblebees travel long distances to good patches of forage, they generally are not foraging during their journey to or from their forage patch. In fact, in Europe they are often forced to cross large areas of crops with little or no reward to reach forage (Walther-Hellwig & Frankl 2000), and they have been shown to be able to cross barriers such as hedges, forests, and roads to reach their food source (Bhattacharya *et al.* 2003, Kreyer *et al.* 2003, Krewenka *et al.* 2011). They have even been observed 20 km from land over an 80 km stretch of water (Mikkola 1984 *in* Osborne *et al.* 1999). When bees leave their nests they tend to know where they're going, zooming away immediately in the direction of their forage patch (Osborne *et al.* 1999). These data suggest that the habitat between bumblebee nests and bumblebee forage does not necessarily need to be contiguous.

If bumblebee habitat does not need to be contiguous (an idea with is supported explicitly by Goulson *et al.* [2011]), what does this mean for our conservation strategy? It means that a close neighborhood of high quality forage is extraordinarily important, while it also provides some leeway in how large that neighborhood needs to be. Bumblebees are attracted to large patches of good forage (Goulson 2010), and if we put a reasonably sized buffer around our focus plants, there is a good chance that enough flowers will be included to attract the bees. Within these patches it is important that the diversity of flora allows for flowering throughout the season, as bumblebee colonies are long-lived and individuals are more likely to return to a place if forage is available from spring until fall. There is also evidence that queens establish their colonies in areas with high availability of early-season forage (Suzuki *et al.* 2009), and that these sites are often reused over several generations (Michener 2007, pg 105). So there is a chance that colonies may become established within the buffer zones we create around occupied habitat if early-season forage is abundant. Even if the bumblebees nest at some distance away, however, they can still act as pollinators due to their ability to fly long distances and cross barriers.

Thus, bumblebee maximum foraging distances are not crucial when designating buffer distances. Instead, it is simply important that we maintain plant diversity within the protected areas to attract *Bombus* pollinators. While it is challenging to determine the perfect size for protecting a plant community, we can shed some light on ideal buffer distances by looking at the requirements of solitary bees.

*Non-*Bombus *social bees*

While bumblebees are very characteristic social bees, they are not alone. The Meliponini tribe (family Apidae), consists of many tropical social bees, while the tribe Halictini (family Halictidae) includes several social species. These species fall within genera that include both solitary and social species, specifically *Lasioglossum* and *Halictus.* The genus *Xylocopa* (Apidae) is semisocial, meaning that two generations often inhabit the same nest. Some species even exhibit different degrees of sociality depending on where they are within the species' range (e.g. *Halictus tripartitus* [Packer *et al.* 2007]). This intermixing of social and solitary species, as well as our limited knowledge about the sociality of many bees, makes it difficult to characterize the foraging patterns of all social bees.

However, several studies suggest that these social bees can be safely grouped with bumblebees when creating buffer distances. Beil *et al.* (2008) studied foraging distances of a social *Lasioglossum*, and found that it flew much further than predicted by body size. However, they also found that it crossed a barrier (a pine plantation) in order to get to its forage. Krewenka *et al.* (2011) found that *Lasioglossum* were also able to cross hedges. *Xylocopa* tends to have very large flight distances (Pasquet *et al.* 2008), and so it almost certainly crosses barriers when seeking out forage. The Meliponini tribe does not exist in Colorado and therefore does not need to be included in our analysis. Thus, while the above discussion about bumblebees does not specifically include other social bees, it does seem to apply, and we consider all social bees to be included when discussing the possibility of non-contiguous habitat conservation.

Solitary Bees

Introduction

Solitary bees are a far more diverse group than bumblebees, accounting for more than 90% of the approximately 3,500 bee species native to the United States (Mader *et al.* 2011, Scott *et al.* 2011). These c. 3,150 species come from 6 different families and hundreds of unique genera. Within Colorado, 946 bee species in 66 genera have been described and only 23 of these species are bumblebees (Scott *et al.* 2011). Accordingly, a wide range of life history traits, foraging behaviors, and nesting habits are found within the solitary bees. Due to this wide range of characteristics, it is even more difficult to determine typical foraging distances of solitary bees than it is for bumblebees. Therefore, while a few specific distances will be discussed here, the majority of this section of the review will focus on factors that are important to consider while designating buffer distances.

It is important to note that some genera contain both solitary and social species (i.e. *Halictus, Lasioglossum,* and *Xylocopa*). These genera are often grouped together with the purely solitary species, a practice which will be followed here. The social species within these genera were addressed at the end of the bumblebee section.

Methods to determine foraging distance

Many of the methods discussed above to measure *Bombus* foraging distances are also used for solitary bees. Homing is a popular experimental technique, which has been used for several species and has returned distances up to 23 km (e.g. Janzen 1971, Vicens & Bosch 2000). Feeder-training experiments are also commonly applied to solitary bees, and have returned foraging distances between 140 m and 2100 m (e.g. van Nieuwstadt & Iraheta 1996, Kuhn-Neto *et al.* 2009, Zurbuchen *et al.* 2010a, 2010b, 2010c).

Mark-recapture studies are the simplest observational method and have been conducted by marking bees both at the nest and while foraging. When marked while foraging these numbers are subject to the same issues discussed at the beginning of the bumblebee section, specifically that without knowledge of the nesting location it is impossible to know how far the bee traveled to get to the forage it is on. As interpatch flights are generally not indicative of distance traveled from the nest (Dramstad 1996), it is difficult to use these data to answer the questions that we are interested in. Nonetheless, these mark-recapture studies have returned a wide range of foraging distances, from 130 m to 2470 m (e.g. Kapyla 1978, Araujo *et al.* 2004, Franzen *et al.* 2009).

Radio tracking has been successfully implemented for the large *Xylocopa flavorufa.* In this situation the researchers attached radio-trackers to the bees at their forage and tracked them back to their nests. They found that this large carpenter bee occasionally foraged at distances up to 6 km from its nest, though the median distance travelled was 720 m (Pasquet *et al.* 2008).

Another observational technique is pollen analysis. In this case, researchers create a map of all available forage within an area, and capture bees as they are returning to their nests or collect provisioned brood cells. They then analyze the bees' pollen loads and match the pollen to known locations of forage, determining the minimum distance the bee must have flown to reach that specific plant. Maximum foraging distances observed using this technique range from 180 m to 1250 m (e.g. Rust 1990, Hembach 1993 *in* Zurbuchen *et al.* 2010c, Westrich 1996, Beil *et al.* 2008).

Finally, foraging distances have occasionally been reported from studies which did not track specific bees at all, only noted that the bees seemed to live within their forage. Using this method, two bees were observed to forage within 50 m of their nests (Westrich 1996, Miliczky 2008).

Altogether, a huge range of solitary bee foraging distances have been reported using a variety of techniques on a diverse selection of bee species. The question is how to relate these numbers to our pollinators and our ecosystems.

Problems with grouping taxa

Just as it is irresponsible to group bumblebees and solitary bees together when determining forage distances, there are certain solitary bee groups that should not be included in our analysis. The primary group that we ought to exclude is the cleptoparasites. These bees do not provision their own brood cells, instead laying their eggs in others' pre-prepared nests. Thus, they don't actively forage for pollen and are unlikely to be providing important pollination services to any plants. While they are important to conserve for their own unique value, they don't play a role in the pollination puzzle and shouldn't be considered when creating buffers.

The second group that it is important to separate out is the tropical bees. Tropical bees include the stingless bees (Meliponini), Euglossine bees, and many *Xylocopa* (carpenter bees). Many flight and foraging distance studies have been conducted on these species (i.e. Janzen 1971, Roubik & Aluja 1983, van Nieuwstadt & Iraheta 1996, Araujo *et al.* 2004), often returning extraordinarily high results. Indeed, these studies create outliers in many graphs, reporting flight distances of up to 23 km (Janzen 1971). These data can be explained, however, by the ecosystem in which tropical bees live and forage. The tropics are characterized by extremely low species density, and individual conspecific trees may be separated by 100 m or more (Janzen 1971), forcing a foraging female to travel very long distances in between hosts during each foraging trip. The ecosystems in which our focus plants grow are very different, as forage is generally much more readily available. Bees in the temperate zone are usually not required to fly such long distances, as is demonstrated by a simple comparison of observed flight distances. While foraging distances of tropical v. temperate bees have not been specifically compared in any literature I was able to find, Araujo *et al.* (2004) found that flight distances of stingless bees (found in the tropics) could be predicted by wing size. They also included IT spans for each species in their paper, allowing their data to be compared to those of Greenleaf *et al.* (2007) (see Fig. 3). The trends displayed by this figure are clear - bees of approximately the same size tend to fly farther in the tropics than in the temperate zone. Therefore, in order to maintain the integrity of our results, it is important to exclude tropical bees from our analysis and from our buffer distance calculations.

Do maximum flight distances accurately predict foraging distances?

Once we have excluded those species that are not even potential pollinators of our rare plants, we still must look at how relevant the available data are. Most studies attempt to determine the maximum flight distance (generally through experimental methods such as homing), and such numbers are what were used to create the equations by Greenleaf *et al.* (2007) and Gathmann and Tscharntke (2002). However, there is a good deal of evidence that the maximum flight (or forage) distances are achieved by only a few individuals (Zurbuchen *et al.* 2010c), and that there are significant fitness costs for those that do fly such long distances (Peterson & Roitberg 2006, Williams & Kremen 2007, Zurbuchen *et al.* 2010b). Many studies with long reported flight distances reflect this, reporting max flight distances that were only reached by a few individuals, and with median flight distances significantly shorter (i.e. Pasquett *et al.* 2008 report a maximum foraging range for *Xylocopa flavorufa* of 6,040 m, while the median distance flown was only 720 m). While Beil *et al.* (2008) report much longer foraging distances for small solitary bees than predicted by Greenleaf *et al.* (2007), these distant resources were only reached on c. 10 of 558 foraging trips. This trend is the thesis of Zurbuchen *et al.* (2010c), who summarized available maximum flight distances of solitary bees and found that they were often higher than predicted by Greenleaf *et al.* (2007). However, they continue, because such a small number of individuals actually fly the maximum distance, the distance at which 50% of the population forages is a much more useful tool for conservation. As very few studies have quantified this, they conclude by stating that a “close neighbourhood of suitable nesting sites and flower rich foraging habitats may be crucial for maintaining populations of bees.” (Zurbuchen *et al.* 2010c).

Other studies demonstrate wide gaps between maximum homing distance and typical foraging distance. For example, *Osmia cornuta* has been shown to return to its nest from 1.8 km away, but it forages within 100-200 m of the nest when forage is readily available (Vicens & Bosch 2000). van Nieuwstadt & Iraheta (1996) state that “more than 75% of the foraging activity normally occurs within 40% of the maximum foraging distance.” Zurbuchen *et al.* (2010c) performed feeder-training experiments on two species of solitary bees, and found that while the maximum foraging distances were 1100 m and 1400 m, 50% of the individuals stopped foraging before 225 m and 300 m, respectively. So despite the fact that many species are capable of traveling long distances, few individuals do. Why is this?

Hypotheses have been presented suggesting that long flight distances have detrimental consequences for an individual’s health and life span (Williams & Kremen 2007, Zurbuchen *et al.* 2010b), perhaps through wear on the wings (Torchio & Tepedino 1980). While these ideas are difficult to test, several more recent studies have shown that reproduction is negatively impacted (Peterson & Roitberg 2006, Williams & Kremen 2007, Zurbuchen *et al.* 2010b). This is due to the fact that females are able to provision fewer brood cells if they are forced to expend more time and energy flying long distances to their forage. In some cases, if a nest is too distant from the bee’s forage the female will be unable to create enough brood cells to replace herself, making the population unsustainable (Zurbuchen *et al.* 2010b). The brood cells that she does provision may also contain less pollen, leading to higher offspring mortality (Zurbuchen *et al.* 2010b). Finally, beyond a lower reproductive count, long distance flights can also skew the sex ratio of a population (Peterson & Roitberg 2006), as males are smaller and require less pollen to grow to maturity.

If few individuals fly long distances to forage, and those that do are penalized, the natural conclusion is that generally solitary bees must nest near their food source. This knowledge makes it clear that creating buffer distances based on maximum flight capabilities is not necessary. The majority of bee nests are likely to be within comfortable flying distance of the bees’ forage, making the distance at which 50% of bees stop foraging a much more useful number. Even if we accidentally separate a bee nest from our plants, solitary bees have been shown to cross barriers to get to their forage just as bumblebees have (Zurbuchen *et al.* 2010a). All evidence is pointing towards maintaining small, resource rich habitat parcels around our rare plants in order to account for solitary bees. But we have to be careful: how small is too small?

A second look at Greenleaf et al. (2007)

To determine appropriate buffer distances that will maintain solitary bee pollination services, we return to Greenleaf *et al.* (2007). This time, however, rather than taking their data at face value we manipulate it to reflect everything that has been discussed thus far in this review. First, a look at the data used to create their equation that predicts homing distance. When all of their data points are included, the resulting graph doesn’t reveal very much about an ideal buffer distance (Fig. 4). However, when we limit the graph to only solitary bee genera traditionally found in Colorado by removing the bumblebee, tropical bee, oil-collecting bee (*Dasypoda altercator*), and carpenter bee (*Xylocopa virginica*), the graph is very different (Fig. 5). (As a side note, *Xylocopa virginica* has recently been documented in Colorado [Scott *et al.* 2011]. However, this represents an expansion of its range, and no *Xylocopa* are recorded pollinators of our focus plants. They are very large bees, with lengthy recorded flight distances. If they do become pollinators of our focus plants at some point in the future, it is likely that they will be able to cross barriers/development in order to reach the plants.)

Essentially, what we have done in figure 5 is to remove the outliers. The data that are left tell a compelling story. Most notable is the fact that only two bee species exhibited “typical” homing distances (the distance from which 50% of individuals return) that were greater than 500 m. This provides a sound platform from which to explore appropriate buffer distances. If other studies also suggest that many native solitary bees forage at or under 500 m, this could be a perfect buffer zone for their preservation. To explore this possibility, we utilized the extensive pollinator flight distance summary provided by Greenleaf *et al.* (2007) in their supplementary materials (their Table S3).

Figure 6 shows a subset of the observed flight distance data that were summarized by Greenleaf *et al.* in the third table of their supplement. In this graph, as in figure 5, all bumblebees and tropical bees have been removed. The single honeybee point was also excluded. Following the above discussion about the importance of using observational methods, we also removed all data points from studies that used manipulative techniques, meaning that there are no data points from homing or feeder-training experiments. Finally, we chose not to include any of the distances gathered from “nest-forager association” studies. This technique attempts to locate all nests and foraging bees of a specific species, then measures the distance between the located bee and the nearest known nest. However, the distances that were reported using this technique were often very large (up to 11.3 km for a medium sized *Nomia*), and Greenleaf *et al.* (2007) report that “it was not clear that all nests in the area had been located.” Because it is notoriously difficult to locate bee nests in the field (Goulson 2010), we assume that the reported flight distances were likely to be large overestimates, and have chosen to exclude them. In the figure that is left, 2/3 of the bees foraged within 500 m of their nest (Fig. 6). While this is admittedly not all of the bees, we feel that it is a common enough trend to base our conservation recommendation on. If we protect 500 m of habitat on all sides of our rare plant species, we should be able to preserve the nests of at least 2/3 of the potential solitary bee pollinators while also preserving enough forage to attract the pollinators whose nests are outside of this buffer zone.

Recommendations

Finding a balance

When an organization such as the BLM is in charge of managing such a large amount of land, maintaining balance is a concept that comes up over and over again. Due to our multiple-use mandate, it is imperative that we account for many different interests. We want to protect rare plants, and use the best possible science to do so. However, we also must permit some development. Clearly, the best thing for natural systems is often for humans to leave them well enough alone. But, in the case where this is unreasonable, we want to protect the plants from harm as best we can.

We must be judicious when deciding how much protection the plants need, however. An initial draft of a recent study by BIO-Logic, Inc suggests that there are few to no discernible negative effects on *Physaria congesta* or *P. obcordata* reproduction indirectly caused by oil and gas development in the Piceance Basin (Graff 2012), and several ongoing monitoring studies by the BLM show that some other populations of rare plants are doing quite well. Total plant density of *Astragalus osterhoutii* in one location, for example, has shown a steady increase over the past 7 years. During this time it is also important to note that neither the number of flowering stems nor the number of fruiting stems have decreased, suggesting that pollination is not suffering (BLM data, unpublished). Both total number of stems and the number of reproductive stems of *Penstemon debilis* have remained steady over the past 8 years at Anvil Points, and in some years the ground has been littered with seeds (BLM data, unpublished). While only two years of monitoring have been completed to date for *Penstemon penlandii*, we have recorded an increase in the number of rosettes in each plot (BLM data, unpublished). None of these plants appear to be showing any signs of pollen limitation with the protections that they currently enjoy, which belies the need to create large buffers around them now.

As we have seen no catastrophic declines in our focus plant species, we must be moderate while creating buffers. We are currently carefully monitoring many of the focus species of this review, and have plans to expand our monitoring program. Thus, these ongoing monitoring efforts will alert us if there are any population declines. If we observe any such declines, we will certainly reevaluate and attempt to determine whether buffer distances need to be extended. However, we believe that implementing the proposed buffer distance of 500 m will avoid any such declines, and will instead maintain healthy populations of our rare plants.

A new approach

Our knowledge of the important pollinators for each focus plant species is patchy at best. When combined with our lack of knowledge regarding bee species-specific foraging distances, it seems presumptuous to create plant species-specific buffer distances. This is compounded when changing species composition between years and network resiliency is taken into account. Thus, as we have shown in this review, the currently proposed buffer distances from the FWS are insufficient. Instead, we have developed a recommendation that takes the very different foraging strategies of social and solitary bees into account. Our proposed buffer distance can be applied to all of our focus plant species which depend on native bees for pollination, thereby protecting the entire pollinator community while also simplifying the protection process.

A 500 meter buffer distance

In order to reach the buffer distance of 500 m, we reviewed the important literature regarding social and solitary bee flight distances. We found that some bees (especially bumblebees and other social species) are able to fly extremely long distances. However, there is compelling evidence that their habitat need not remain contiguous. Instead, it is most important that the protected habitat is large enough to maintain enough floral diversity to attract these far-flying pollinators. If the early-season forage is rich enough, it may entice bumblebees to nest within the protected area, and even if the queens don't choose these protected areas as nest sites, they are still large enough to attract foraging bees.

While researchers have also reported long solitary bee foraging distances, the majority of individuals remain near the nest. This is probably due to high costs associated with long foraging trips; including fewer provisioned brood cells, increased offspring mortality, and skewed offspring sex ratios. When Greenleaf *et al.* (2007)'s data are corrected to remove social bees, bees not found in North America, and data points from manipulative experiments, they show that the typical foraging distance for many solitary bee species seems to be less than 500 m.

Five hundred meters on all sides of occupied habitat almost certainly will create an area that is large enough to maintain floral diversity. Thus, beyond allowing solitary bees to nest within protected habitat, it should also provide a tempting patch of flowers for any social bees that nest nearby. Overall, 500 m seems to be both a reasonable and a responsible buffer distance that will protect the entire pollinator community around Colorado rare plants.

Tables and Figures

Species	FWS Proposed Set-back (m)	Observed Insect Visitors	Status	Endangered Species Act	BLM Sensitive?
Astragalus microcymbus	500	2	G1/S1	Candidate	Yes
Astragalus osterhoutii	1000	5	G1/S1	Endangered	No
Eriogonum pelinophilum	250	37	G2/S2	Endangered	No
Eutrema penlandii	500	0	G1G2/S1S2	Threatened	No
Penstemon debilis	1000	54	G1/S1	Threatened	No
Penstemon grahamii	500	9	G2/S1	Proposed	No
Penstemon harringtonii	n.a.	0	G3/S3	None	Yes
Penstemon penlandii	1000	28	G1/S1	Endangered	No
Penstemon scariosus var. albifluvis	500	13	G4T1/S1	Candidate	Yes
Phacelia formosula	500	15	G1/S1	Endangered	No
Phacelia submutica	100	0	G4T2/S2	Threatened	No
Physaria congesta	600	4	G1/S1	Threatened	No
Physaria obcordata	600	22	G1G2/S1S2	Threatened	No
Sclerocactus glaucus	700	7	G3/S3	Threatened	No
Spiranthes diluvialis	800	24	G2G3/S2	Threatened	No

Table 1. The focus plant species of this review. “FWS Proposed Set-back” distances have been drawn from the FWS draft guidance for Section 7 consultations and are equivalent to the buffer distances discussed in this document. *Penstemon harringtonii* is not recognized under the Endangered Species Act and therefore not included in the Section 7 consultations document. Observed insect visitors are a count of all insect species that have been reported visiting each species. (Compiled from: Karron 1987, McMullen 1998, Naumann *et al.* 1988, Heil & Porter 1990, Warren 1990, Sipes & Tepedino 1995, Rechel *et al.* 1999, Tepedino *et al.* 1999, Pierson *et al.* 2000, Lewinsohn & Tepedino 2004, Lewinsohn *et al.* 2005, Tepedino 2008, Tepedino 2009, Service 2011b, Tepedino *et al.* 2011)

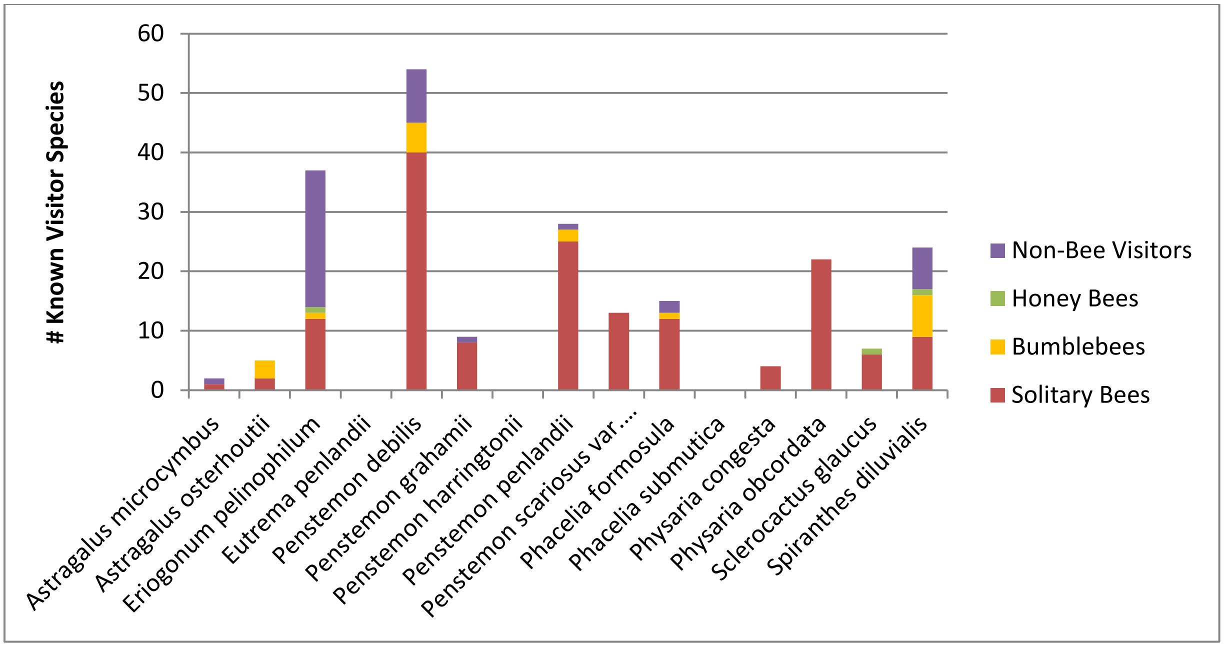

Figure 1. Recorded observed visitors to each of the 15 focus plant species. Bars represent the number of species observed, not the number of individuals. No insects have been recorded visiting *Eutrema penlandii, Penstemon harringtonii*, or *Phacelia submutica*, but this reflects a lack of information, not necessarily a lack of pollinators. The studies included followed different methodologies and expended different amounts of effort. Therefore this graph demonstrates both the wide variation in what is known and the possible differences between visitor compositions (but see "Why the status quo is insufficient"). (Compiled from: Karron 1987, McMullen 1998, Naumann *et al.* 1988, Heil & Porter 1990, Warren 1990, Sipes & Tepedino 1995, Rechel *et al.* 1999, Tepedino *et al.* 1999, Pierson *et al.* 2000, Lewinsohn & Tepedino 2004, Lewinsohn *et al.* 2005, Tepedino 2008, Tepedino 2009, Tepedino *et al.* 2011)

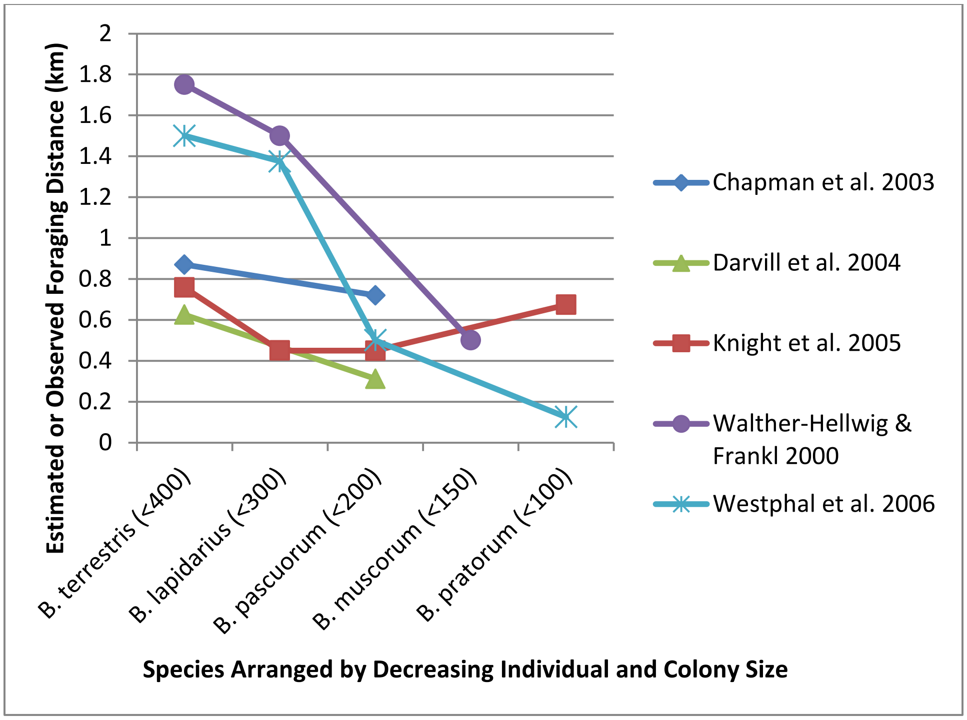

Figure 2. Estimated or observed foraging distances from all studies that compared multiple *Bombus* species. Species are arranged by both decreasing body size (from Knight *et al.* 2005) and decreasing colony size (from Goulson 2010). Average colony size is in parentheses after each species. The foraging distances from Westphal *et al.* (2006) follow the interpretation found in Goulson (2010), while the foraging distances depicted from Chapman *et al.* (2003) are the lower limits of their maximum foraging range estimates. This graph is best used to compare interspecific trends rather than to determine actual foraging distances, as not all data from the studies are included. (Compiled from: Walther-Hellwig & Frankl 2000, Chapman *et al.* 2003, Darvill *et al.* 2004, Knight *et al.* 2005, Westphal *et al.* 2006)

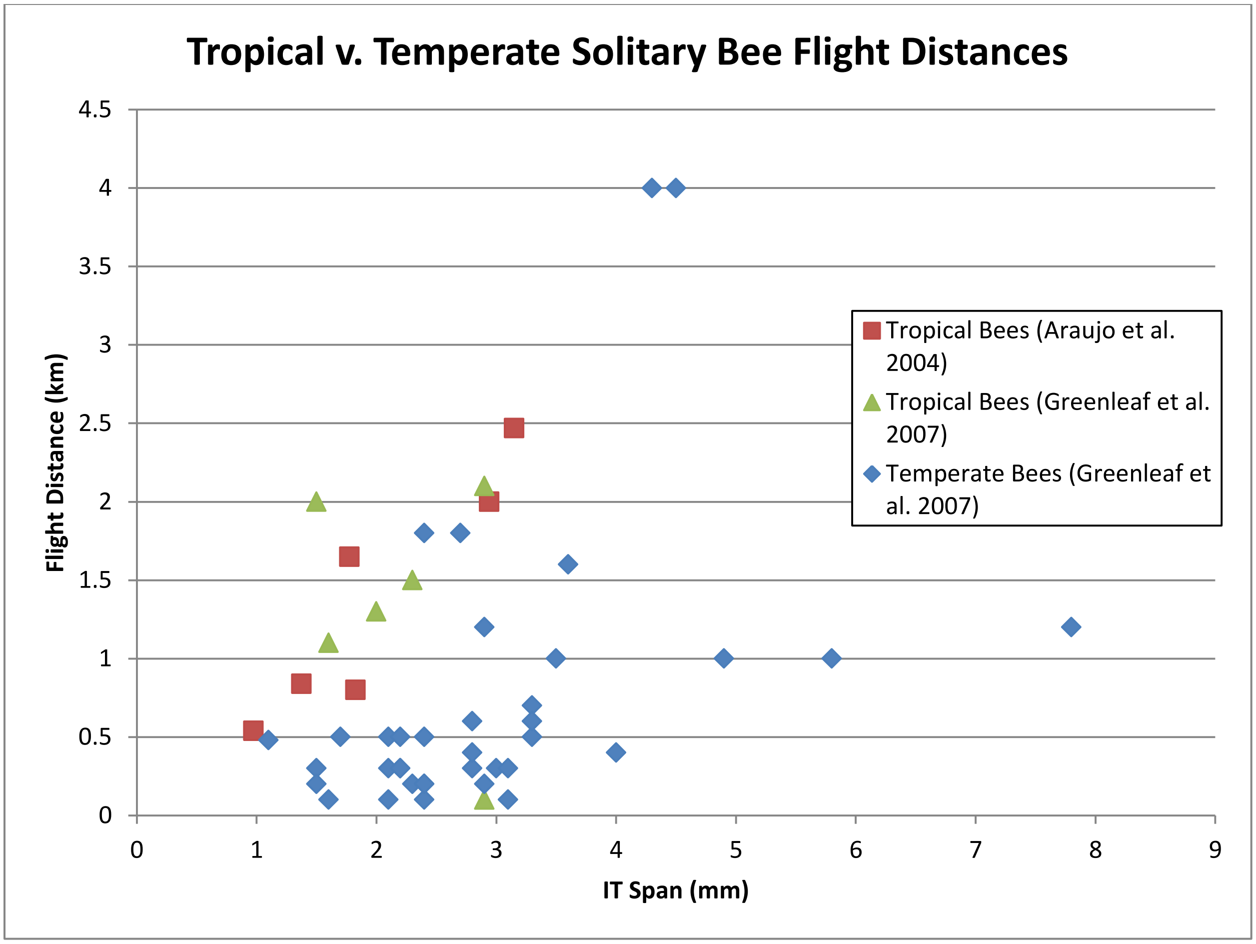

Figure 3. Demonstrates the different flight distances observed for solitary bees found in the tropics v. those found in temperate zones. With a few anomalies, bees of equivalent size fly farther in the tropics. Data are from Araujo *et al.* (2004) and from observed flight distances in Table S3 from Greenleaf *et al.* (2007), which summarizes many other studies. Bumblebees, a single honeybee, and distances found by nest-forage association techniques were not included in this graph. Reasons for these omissions can be found in “A second look at Greenleaf *et al.* (2007).”

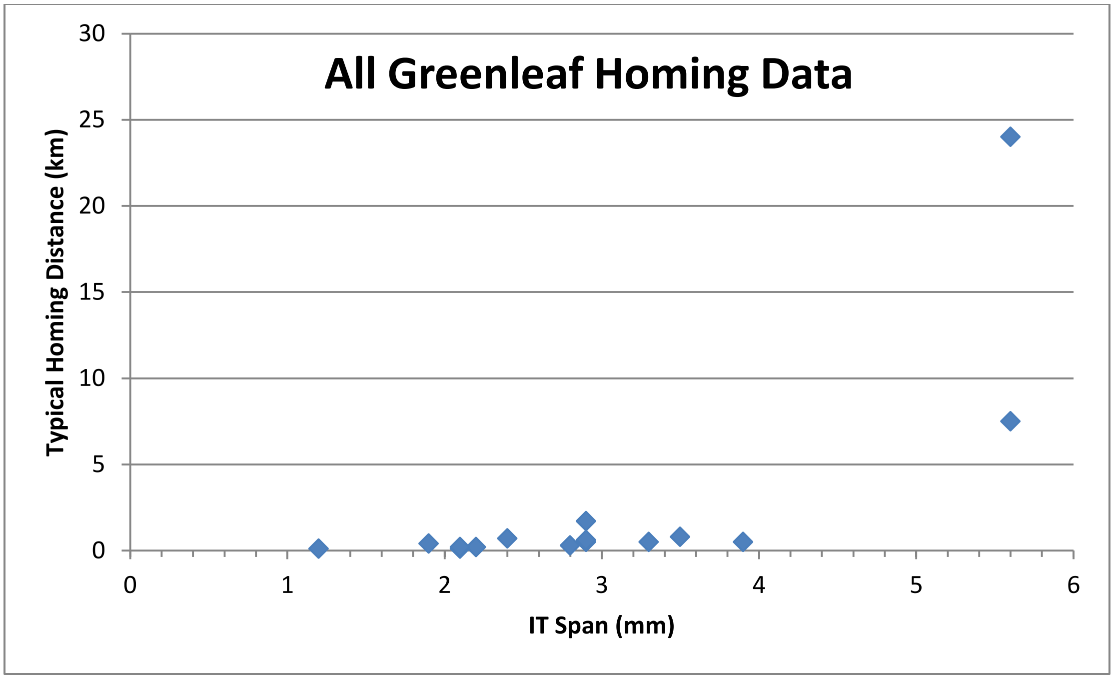

Figure 4. "Typical" homing distance (distance from which 50% of bees return) for all species used by Greenleaf *et al.* (2007) to create their homing distance equation. (Data from Greenleaf *et al.* 2007 supplementary materials Table S3).

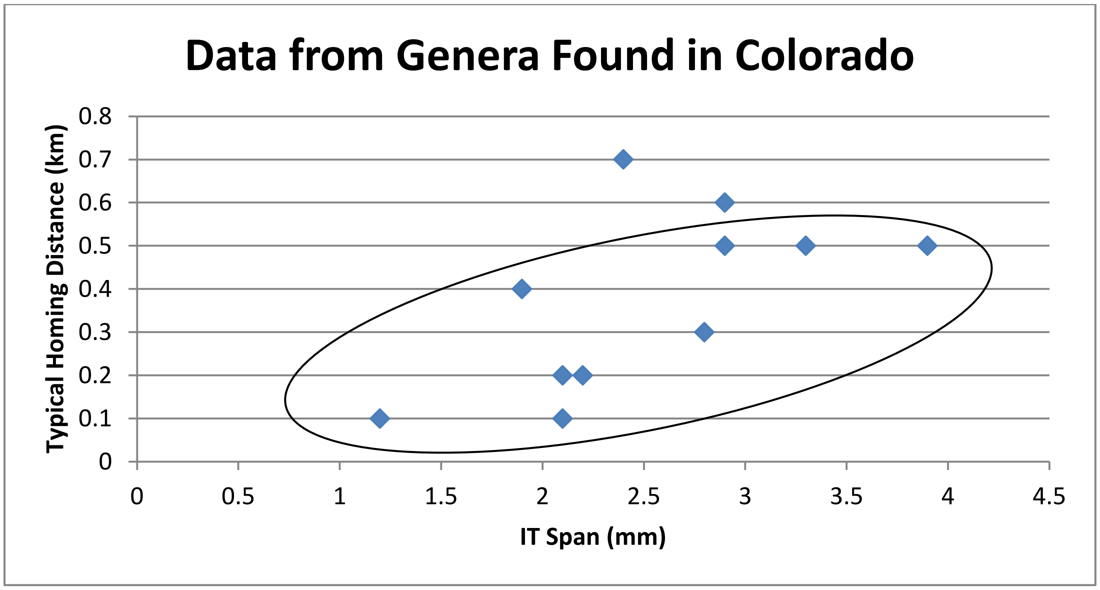

Figure 5. Typical homing distances of the genera found in Colorado that are used by Greenleaf *et al.* (2007). The oval encompasses all points which are 0.5 km or less. Points from a bumblebee, tropical bee, oil-collecting bee, and carpenter bee were removed. (Data from Greenleaf *et al.* 2007 Table S1)

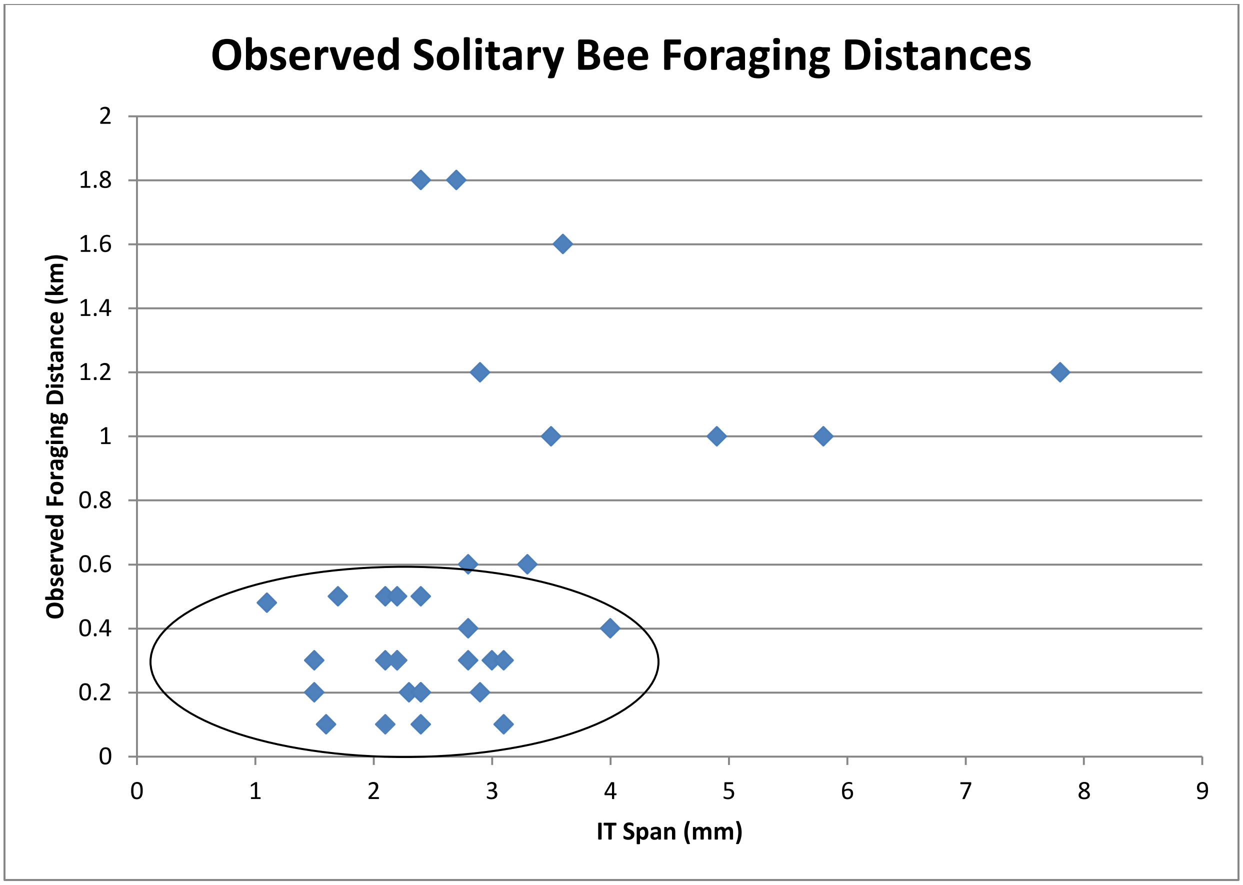

Figure 6. A subset of observed solitary bee flight distances summarized in Table S3 (from Greenleaf *et al.* 2007). The oval encompasses all foraging distances equal to or less than 0.5 km. Data not included in this graph were from bumblebees, tropical bees, or were found via manipulative or nest-forage association techniques. The reasons for excluding these data are discussed in the text.

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