

THE EFFICACY OF SAGUARO CACTUS (*Carnegiea gigantea*) POLLINATION SYSTEMS

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ABSTRACT

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Caitlin Winterbottom

One of the most charismatic plants in the Sonoran Desert is the giant columnar cactus characteristic of the southwest. Saguaro cacti (*Carnegiea gigantea*) dominate this landscape, and many animals depend on their flowers and fruits. Adequate visitation to saguaro flowers will result in adequate fruit and seed set, which is critical for the future success of this iconic species. The development of Colossal Cave in 1961, once a suitable maternity roosting habitat for lesser long-nosed bats (*Leptonycteris curasoe*), resulted in an absence of this species during spring and early summer causing the timing of saguaro flowering and the presence of these bats to no longer overlap (Bat Conservation International). Given changes in the presence and reliability of lesser long-nosed bats as pollinators of saguaro, an updated investigation of the efficacy of these pollinator communities was necessary. The overall “effectiveness” of a pollinator can be divided into two parts – quantity & quality, quantity being the visitation rate and quality being the pollination services the pollinator is providing. I conducted over thirty hours of pollinator observations to assess overall diversity and abundance of different pollinator functional groups. My analyses found that birds exhibited the best quantity of visits to saguaro as they visited large quantities of flowers in a short time, especially when compared to slower and more methodical foraging strategies of bees. Additionally, I implemented bagging experiments to better understand what pollinator groups contributed to the reproductive output of saguaro in the form of seed set. The results of this experiment indicated that 80% of seed set in saguaro can be attributed to bee pollination, whereas the other 20% is attributed to birds. There was not a significant difference between bagging treatments which indicated that saguaro is not pollen

limited, they are self-incompatible, and these data also support that there was little to no nighttime pollination occurring. Birds may visit large quantities of flowers when they visit saguaro, but bees were clearly more impactful in their quality of pollination services and thus contribution to seed set. Fortunately, saguaro have reliable diurnal visitors that are pollinating them effectively, regardless of the absence of their nocturnal pollinators. Understanding interactions of keystone species, such as the saguaro, will become increasingly important given future changes in climate predicted for this region of the southwest, which could lead to the potential disruption of important plant-pollinator relationships.

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INTRODUCTION

The Sonoran Desert of northern Mexico and southern Arizona is one of the most biologically diverse deserts in the world (Fleming 2001), rich with unique species that have adapted to tolerate the intense heat. One of the most charismatic plant groups in this system is the towering columnar cacti characteristic of the Southwest (Marazzi et al. 2015). Saguaro cacti (*Carnegiea gigantea*) dominate this landscape, and many animals depend on their flowers and fruits. Saguaro is a keystone species of the Sonoran Desert (Wolf & del Rio 2000). Saguaro produce large, cream-colored flowers that provide nutrients to the insects and animals that visit them (Fleming 1996; McGregor et al. 1962). The saguaro relies on animal pollinators for fruit and seed set, critical for the reproduction and future success of this iconic species (Franklin et al. 2016). Their fruits are eaten and seeds dispersed by many birds in the Sonoran (Wolf & del Rio 2000). Elf owls (*Micrathene whitney*), Gila woodpeckers (*Melanerpes uropygial*) and a suite of other bird species take advantage of the cavities in saguaro stems to build nests (Inouye et al. 1981; Hardy & Morrison 2001).

Dryland ecosystems like the Sonoran Desert are particularly at risk from projected increases in temperature as their productivity is directly linked to moisture availability (Winkler et al. 2018; Seager et al. 2007; Weiss & Overpeck 2005). Uncertainty regarding future temperature and precipitation events impacts our ability to properly develop management and policy actions to protect these systems (Bradford et al. 2019). Saguaro are CAM plants, like other cacti, and only open their stomata at night. This method of photosynthesis reduces the amount of water lost by the plant by exposing open stomata only to the cooler and more humid nighttime temperatures (Hultine et al. 2016). However, projected changes in temperature and precipitation indicate an increase in the nocturnal temperatures in the Sonoran Desert, which will put greater evaporative demands on saguaro cacti (Williams et al. 2014; Bronson et al. 2011).

Importantly, a key adaptation of cacti is their elevated ability to store water. Their photosynthetic and expandable stems rapidly uptake and store massive amounts of water to support growth, reproduction, and survival during hot and dry periods (Hultine et al. 2016). As extended drought periods become more common in this region of the Southwest, these adaptations are more important than ever for the survival of the saguaro. A changing climate will have a significant influence on the livelihood of complex and diverse Sonoran Desert plant and animal communities, as well as the ecosystem services that they provide (Marazzi et al. 2015). Extreme heat waves or freeze events can cause rapid ecological change in drylands with the potential of killing established plants, or at the very least significantly disrupting their ecological interactions (Renzi et al. 2019).

The seasonal timing of flowering, known as phenology, also plays a significant role in the dynamics of plant-pollinator interactions and is greatly influenced by these changes in climate (O'Neil 1997; Fleming 2006). Numerous studies have shown that timing of flower production can strongly influence pollination success and fruit set (Fleming 2006; Renzi et al. 2019). Sonoran Desert plants have begun to flower earlier or later in the year due to increasing temperatures, which could lead to phenological mismatches, or the disruption of many important mutualistic relationships, if flower and then fruit production become decoupled from pollinator and seed disperser activity (Fleming 2006; Renzi et al. 2019). Indeed, the Arizona-Sonora Desert Museum (ASDM)'s 30-year phenology data set indicates that saguaro's flowering phenology has shifted so flowers are blooming up to three weeks earlier than historically (ASDM 2018; Figure 1). Such a shift has implications not only for the fruit and seed set of saguaro, but also for the animals that depend on them. Even the order of flowering of individual plants within saguaro populations can be important for population dynamics (Renzi et al. 2019). The timing and

variability of flowering could potentially result in limitations on pollen flow (Bustamente & Borquez 2008). The study of saguaro flowering biology is therefore important for conserving the pollinator diversity present in the Sonoran Desert. As many ecosystem services, like pollination, become more susceptible to change, we may see certain species start to decline in their abundance and productivity.

Generalized Pollination Systems

The morphological traits of a flower may indicate the type of pollinators it attracts, a pattern known as a pollination syndrome (Proctor 1996; Fenster et al. 2004). For example, bees are mainly attracted by visual cues and need high sugar concentrations in nectar, hummingbirds are attracted to the color red, and tubular flower shapes, and bats tend to visit flowers that are white and open at night (Lemaitre 2014). Rather than specializing on one species or type of pollinator, some plants may attract more than one type of visitor; these are called generalized pollination systems (Waser et al. 1996; Waser & Ollerton 2006). Generalization is a good strategy for variable environments, where the abundance and diversity of pollinators fluctuates through space and time, as it prevents the plant from being reliant on any one pollinator type (Fleming et al. 2001). For a pollinator to be considered beneficial to a plant in a generalized system, pollinators should directly increase the plant's reproductive output in the form of fruit and seed set (Proteaceae 2020). Both visitation rate and the effectiveness of pollen transfer must be considered when comparing the importance of pollinators in a generalized system (Aigner 2004). Birds and bats are effective visitors of many plant species as they are active in a variety of environmental conditions (e.g., night and day, variable weather, etc.). Additionally, when compared to bees, birds and bats have larger home ranges and increase the possibility of outcrossing for the plants they visit (Krauss et al. 2017). Bats are highly effective visitors

because they can visit a lot of flowers in a short amount of time and their fur is good at trapping and transporting pollen long distances (Muchhala & Thomson 2010). In flight cage experiments bats transferred four times as much pollen as hummingbirds (Muchhala & Thomson 2010). The presence and reliability of bats as pollinators can be unpredictable from year to year in some regions, which is why generalized pollination systems may be favorable for plants (Fleming et al. 2001). Bees are less effective pollinators of many plants compared to bats because they are often foraging for pollen to provision their young, and when mixed with nectar on their corbiculae, pollen is not as readily available for deposition (Lemaitre 2014). Differences in pollination effectiveness among native and non-native bees have been attributed to foraging behavior (Brittain et al. 2013). For example, honeybees are poor pollinators of alfalfa and apples because they visit flowers in a way that allows for nectar and pollen collection without pollen transfer (Abrol 2012).

Functional complementarity of pollination occurs when two or more pollinators visiting flowers result in higher plant fitness compared to single pollinator species on its own (Blüthgen & Klein 2011). Generalized pollination systems can be either complementary where fruit set is limited by the sum of the contributions of individual pollinators, or redundant if one pollinator group can be replaced by another without a loss in fruit set (Fleming et al. 2001). Redundancy can be either total when different groups are completely substitutable, or partial when different groups are not completely substitutable (Fleming et al. 2001). Niche partitioning can occur due to differences in time of day that pollinators are visiting flowers (Alonso-Pedano & Ortega-Baes 2012). For example, both nocturnal and diurnal pollinators visit the flowers of saguaro, and this reduces competition between these pollinators. Functional complementarity in the different elements of pollination could help explain the positive effects of biodiversity in pollination