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Cover: A Snowy Egret "foot stirring" to find prey. The number of foraging Snowies in Bolinas Lagoon increases during fall and winter. Photo by Philip Loring Greene.

Ardeid masthead Great Blue Heron ink wash painting by Claudia Chapline.

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Exploring the dynamics of seasonal wetlands at the Bouverie Preserve

Fountain of Fountains

by Sherry Adams and Arthur Dawson



Figure 1. A measuring tape is stretched (from center foreground) across wetland 5A to prepare for vegetation monitoring. Meadowfoam (*Limnanthes douglasii* ssp *douglasii*), a wetland generalist, is the dominant species.

We know that the wetlands of Sonoma Valley have gone through major changes in the last 200 years. In the very first written description of Sonoma Valley, Father Jose Altimira remarked on the many springs, ponds, marshes, and creeks on the valley floor. Water was noticeably more abundant here than anywhere else he went, including Petaluma, Napa, and Suisun valleys. Altimira was so impressed by this abundance that he nicknamed Sonoma Valley "un manantial a manantiales" or "a fountain of fountains." The abundance of water was one of the reasons he chose to

establish his mission here.

The largest wetland was in the upper part of the valley. Though it was called the Kenwood Marsh, it was really a chain of marshes and wetlands covering about 400 acres and stretching five miles from the watershed boundary (Pythian Road), through present-day Kenwood, to near Dunbar School in Glen Ellen. In fact, this marsh complex extended all the way to the edge of modern-day Santa Rosa, suggesting that a subsurface connection existed—and may still exist—between the Sonoma Creek and Santa Rosa Creek watersheds (Anonymous 1837). Groundwater was exceptionally high throughout this part of Sonoma Valley. Some of the Kenwood Marsh probably held surface water throughout the year (Boggs 1861). By catching runoff from winter storms and releasing it over many months,

Every day, 15,000 cars pass within view of an especially valuable area of habitat at ACR's Bouverie Preserve in Sonoma Valley, yet the area is rarely visited, since no trail leads to it. This habitat fluctuates wildly through the course of the year. During the winter rains, plants germinate and insects and other tiny invertebrates enter into the aquatic phase of their lives. In spring these spots slowly dry out, wildflowers bloom, grasses grow, and frogs hop off on new legs. This is followed by complete desiccation, with a handful of specially adapted plants, such as the aromatic vinegar weed (Trichostema lanceolatum), growing and flowering in the heat of summer. This dynamic habitat is the wetlands of Lower Field of the Bouverie Preserve (Figure 1).

In addition to the changes this habitat goes through in the course of a year, it can

look quite different from one year to the next. For example, in most years the Bouverie wetlands are home to over 100,000 individuals of the rare vernal pool wildflower, dwarf downingia (*Downingia pusilla*), but in 2009, due to the unusual winter precipitation pattern, only about 14,000 were present. Like other annual plants, this one has a large seed bank and is expected to thrive again when the conditions are supportive. This sort of interannual variation is expected in the natural world.

Each time we consider changes at a different temporal scale, the patterns we have previously focused on may fade from view, and new ones become apparent. If we take one more step back, to consider changes within a timeframe of decades to centuries, what patterns overshadow these well-known yearly cycles and year-to-year fluctuations?

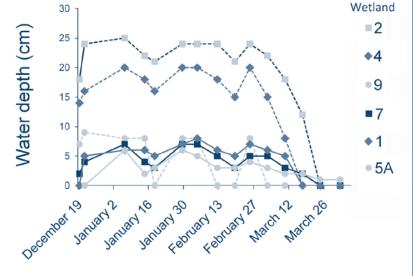


Figure 2. Maximum water depths at several wetlands during winter, 2007–2008. Wetlands with a dashed line have greater swings (flashier hydrograph) than those with a solid line.

the Kenwood Marsh acted as a sponge, reducing downstream flooding and increasing the flow of Sonoma Creek during the summer dry season.

Investigating Bouverie Preserve wetlands

At the Bouverie Preserve we wanted to know more about our wetlands, including how they may have changed over time. We knew there were some seasonal wetlands in the grassland that borders the highway, but we had no detailed information about the hydrology. We suspected that the wetlands were all vernal pools in various states of degradation. We hypothesized that the shallower wetlands may once have been deeper and then suffered from silt accumulation caused by management practices in a former era.

The majority of vernal pools in California have been destroyed (Holland 1978), and the remaining ones are home to rare species. Because degraded vernal pools are an area of great conservation concern, we were able to secure funding to investigate the nature of the wetlands of the Lower Field. The investigation involved four activities. First, we marked the deepest part of each wetland and then, during the rainy season, revisited that location each week to measure water depth. Second, we conducted springtime vegetation surveys and used grazing, prescribed fire, and mowing to control introduced European grasses in the different portions of the Lower Field. Third, to

look for evidence of silt accumulation, we asked Dr. Steve Talley, a soil scientist with extensive vernal pool experience, to investigate the wetland soil conditions. Finally, we inspected modern and historic aerial photos for evidence of wetland modification.

Hydrology

We found two types of wetlands in the Lower Field of the Bouverie Preserve. One

type quickly fills when it is raining, and the water level drops between precipitation events. This is consistent with the explanation that these wetlands have a mostly impermeable clay hardpan bottom (as with vernal pools). Rainwater collects in them and then evaporates (Figure 2, dashed lines). The second type of wetland never holds much water (less than 10 cm), and the water level rises only slightly in response to rain events, dropping slowly afterwards (Figure 2, solid lines).

Vegetation

In the first type of wetland, the one with a flashier hydrograph, or greater upand-down swings in charted water level, characteristic vernal pool species were present. In the second type of wetland, the one with lower, more stable water levels, characteristic vernal pool species were not found. Instead, these areas were dominated by grasses and grass-like species (sedges and rushes). After mowing or grazing, we saw some native wildflowers in this second type of wetland, but these were not vernal pool specialists. Rather, they were wetland generalists such as meadowfoam (Limnanthes douglasii ssp douglasii; Figure 1) and marsh monkeyflower (Mimulus guttatus).

Wetland 9 (Figure 3) is shallow, no deeper than our second group of wetlands, the wet meadows (Figure 2). Yet after we used prescribed fire in 2007 to minimize the growth of grasses in this area, the rare vernal

Table 1. Characteristic vernal pool species and generalist wetland species of the Bouverie Preserve, and the wetlands in which they are found. See Figure 3 for the locations of numbered wetlands.

	Wetland					
	2	4	9	7	1	5A
Vernal pool species						
water pygmyweed (Crassula aquatica)	\checkmark					
calicoflower (Downingia concolor)	\checkmark	\checkmark				
dwarf downingia (Downingia pusilla)	\checkmark	\checkmark	\checkmark			
coyote thistle (Eryngium aristulatum)	\checkmark	\checkmark				
quillwort (Isoetes howellii)	\checkmark	\checkmark				
popcorn flower (Plagiobothrys stipitatus)	\checkmark	\checkmark				
wolly marbles (Psilocarphus brevissimus)	\checkmark	\checkmark	\checkmark			
pacific foxtail (Alopecurus saccatus)	\checkmark					
Generalist wetland species						
meadowfoam (Limnanthes douglasii)	\checkmark	\checkmark	\checkmark	\checkmark	\checkmark	\checkmark
marsh monkeyflower (Mimulus guttatus)				\checkmark	\checkmark	\checkmark
iris-leaved rush (Juncus xiphioides)			\checkmark	\checkmark	\checkmark	\checkmark

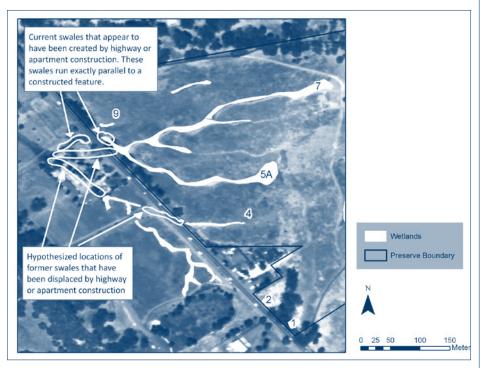


Figure 3. Wetlands of Bouverie Preserve's Lower Field and adjoining lands. Numbers indicate individual wetlands. Highway 12 crosses from the upper left to lower right of the aerial photo.

pool specialist dwarf downingia was present. We did not introduce this species, so its presence in wetland 9 suggests that the seed bank of these wetlands is long-lived and can provide clues to the history of these sites.

Soil investigations

We found no evidence that the wetlands were once deeper and have been filling in, though it is impossible to rule this out completely, based on the soil investigations. In some wetland areas of the Lower Field, including wetland 1, Dr. Steve Talley (2008) observed soil mottling, indicating a long history of wetting and drying (Figure 3). During the course of excavating soil pits, he discovered that wetlands 7 and 5a, which have water levels that fluctuate less than the typical vernal pool's, are fed by subsurface seeps. He also found no mottling in the swale that parallels the highway, suggesting this swale may not be natural and was created as a byproduct of highway construction (Figure 3).

Photographic investigations

Modern aerial photos of the area show swales that end abruptly at roads and property boundaries. Other swales dead-end after short stretches where they run exactly parallel to constructed features like the highway and an apartment complex (Figure 3). An historic photo from the U.S. Department of War indicates this pattern was already evident in 1942.

Putting together all the pieces

We found no evidence to suggest that the hydrology of the Bouverie wetlands has been affected by silt accumulation. The hydrological, biotic, and edaphic (soils) evidence revealed two distinct types of wetlands in the Lower Field of the Bouverie Preserve. The wetlands with flashier hydrographs are appropriately called vernal pools because of their characteristic vegetation and the likely presence of a clay hardpan associated with highly variable water depths (dashed lines in Figure 2). In our system, these vernal pools are primarily fed by overland flow of rainwater. The other type of wetland we have is wet meadow. Their hydrographs suggest that our wet meadows are fed primarily by the subsurface flow of ground water (solid lines in Figure 2).

The basic sources of water for these two types of wetlands, precipitation and subsurface flow, have probably not changed over time, since they are dictated by the soil and subsurface water patterns. However, about five years ago the preserve had to deepen its well, so we know that there have been significant local changes to the ground water level. What has happened to Altimira's "fountain of fountains?" Agricultural and residential development has played a large role in draining the land. Gutters, ditches, and hard surfaces shunt winter rains quickly through the watershed to the bay and ocean. Flooding is reduced, but so is the groundwater that sustains our creeks and wetlands. Historical investigations suggest that since 1823, Sonoma Valley has lost more than 95% of its freshwater wetland area (Dawson et al. 2008).

Based on our field observations, the patterns evident on the aerial photograph, and documented historical trends in the wetlands of the Sonoma Creek watershed, we think that the main ways our wetlands have changed are in the reduction of their extent, the loss of hydrologic connectivity, and, possibly, a reduction in the number of days of inundation each year. They may have once been one small part of a large complex of wetlands in Sonoma Valley. The Bouverie Preserve provides a home for this relict habitat and its resident species, now rare in Sonoma County.

For every answer suggested by an ecological mystery, new questions arise. Did our seasonally wet meadows previously remain wet for a greater part of the year? The wet meadows are currently dominated by introduced invasive species. What plant species previously dominated our wet meadows, and what animal species called them home? In general, wetlands provide important ecosystem services, by filtering nutrients and pollutants, providing flood control, and sustaining natural environmental conditions that humans value. What ecosystem services do our wet meadows provide?

We are grateful to the US Fish and Wildlife Service Private Stewardship Grant Program, The Community Foundation of Sonoma County, and the Rockey Family Foundation for funding grassland restoration work at the Bouverie Preserve. Conversations with soil scientist Steve Talley informed this article.

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Strategic nest attendance by Great Egrets

The Ecology of Parental Wisdom

young unattended

at the nest. We are

currently working to

understand this paradox, by investigating

just how Great Egrets

(Ardea alba) nesting at

ACR's Bolinas Lagoon

Preserve schedule their

nest attendance duties

to maximize their abil-

ity to fledge healthy

young (Rothenbach

the nesting cycle,

from "guardian" to

"post-guardian" nest

attendance behavior.

During the guardian period, parents share

incubation duties by

alternating their time

together, they attend

the nest continuously.

After the eggs hatch,

take turns attending

ing. When one parent

arrives at the nest with

food for the nestlings,

the nest and forag-

adults continue to

at the nest so that,

tion).

and Kelly, in prepara-

Midway through

herons and egrets shift

by John P. Kelly and Christine A. Rothenbach



When young egrets reach three to four weeks of age, parents must weigh competing challenges of guarding the nest against predators and gathering food from surrounding wetlands.

I once watched a pair of ravens land next to a Great Egret nest that was occupied by two unguarded chicks. Immediately, the ravens proceeded to harass the young birds. After dodging several bill-thrusts from the defensive egret chicks, one of the ravens grabbed a nestling by its bill, pulled it down, and killed it. Although events like this seem gruesome, they are not unusual in heronries. Chicks guarded by adults are virtually immune to attack by ravens, but, surprisingly, herons and egrets typically leave their the other takes off to search for more food. When Great Egret nestlings reach three to four weeks of age, both parents begin to forage for food simultaneously. This combined feeding effort provides young with more food but leaves them unguarded except during brief, frenzied feeding episodes. As nestlings grow, they become more defensive and the likelihood of nest predation declines, but younger, smaller nestlings can be easily taken by predators. Presumably, the intensified, post-guardian feeding activity gives fledglings a valuable head start. But how much time should parents devote to finding food vs. guarding their young?

The care of parents for their young is common throughout nature, sometimes revealing impressive or even heroic efforts. What interests ecologists is that such care is generally adaptive and often strategic. In birds, patterns of nest attendance are strongly influenced by the developmental needs of their eggs and nestlings, by the challenges of finding enough food to support a family, and by the complex and dynamic behaviors of nest predators. A complete commitment to any one of these concerns, however, can result in the neglect of other needs. So how do egrets determine the best way to manage family responsibilities? As in humans, the best egret parenting is ad hoc and depends on an ability to make wise decisions in response to changing conditions.

How parents make decisions

To examine nest attendance choices, we addressed two hypotheses based on numerous observations of Great Egret nests subject to the risk of predation by resident Common Ravens (Corvus corax). First, we considered the "Trade-off Hypothesis"-that egrets guard their nests continuously, to reduce predation risk, until increasing food demand of the developing nestlings forces both parents to forage for food simultaneously. This idea proposes that the increasing risk of nestling starvation forces parents to leave their nests unguarded. To test this hypothesis, we evaluated how the age of chicks at the onset of the post-guardian period affects reproductive performance.

Under the Trade-off Hypothesis, we predicted that egrets would guard their nests as long as possible and that fewer nests therefore would be taken by predators. We expected that the associated sacrifice of foraging time might reduce the number of chicks produced in successful nests, because some of the young might starve. Among



As nesting egrets grow large, both parents work to meet the increased food demand, returning to the nest only for frenzied feeding visits.

nests that successfully avoid predation, however, those with shorter guardian periods should be able to raise more young. We also expected a narrow range of chick ages at the onset of the post-guardian period, because parents might guard their nests until their young reach some critical age when food demand forces both parents to search for food. Finally, under the Trade-off Hypothesis, we expected relatively little synchrony in the onset of post-guardian behavior in the colony, because nests initiated at different times should reach the critical nestling age at different times.

Second, we tested the "Dilution Hypothesis"—that adult egrets in a colony synchronize the time of the season when they begin

to leave their nests unguarded, to reduce the per capita risk of predation by spreading risk across a larger pool of vulnerable nests. Nestlings are more likely to be taken by predators when they are smaller, so the most dangerous time of the season is when the developing young are first left unattended. To test Dilution Hypothesis, we counted the number of other post-guardian nests in the colony on the day when each

nest was first left unattended.

Under the Dilution Hypothesis, we predicted that, in each successful nest, more chicks would be fledged: if reduced per capita risk of nest predation allows parents to focus more time on foraging for food, they may be able to support larger families. We also expected that greater synchrony in leaving nestlings unattended might lead to more nest failures, because any late broods, with relatively small chicks, might be easily taken by predators. Finally, under the Dilution Hypothesis, we expected a wider range of chick ages at the onset of the post-guardian period, a necessary result of synchronizing parental behavior among nests initiated at different times.

Measuring parental behavior

The nesting performance of all breeding pairs of egrets in the heronry has been monitored annually since 1967 (Pratt and Winkler 1985, Kelly et al 2007). For this study, we used nesting data from 19 years (1984,1987–1997, and 2002–2008), excluding years when there was no observed nest predation or when the timing of the postguardian period was not precisely measured.

To focus on the parents' competing challenges of finding food for nestlings and protecting them from predators, we included nests only if they met the following criteria: (1) at least one egg was hatched; (2) nest failure, if it occurred, was caused by predation; (3) the length of the guardian period was precisely determined; and (4) the nest was the first of the season at that nest site and likely to have been the parents' first attempt that season (initiated before colony size began to decline). If an entire brood disappeared between observations, we assumed that it was taken by a predator.

To account for differences in parental behavior between successful and unsuccessful nests, and among successful nests that fledged one, two, or three young, we compared several statistical models (explanations of egret behavior) based on observations of nesting egrets. The models included controls to account for annual differences in colony productivity, intraseasonal timing, and environmental factors such as rainfall or temperature. The analysis also distinguished egret parental behavior between years with and without resident

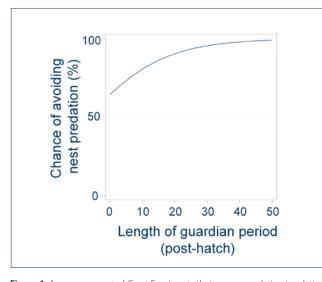
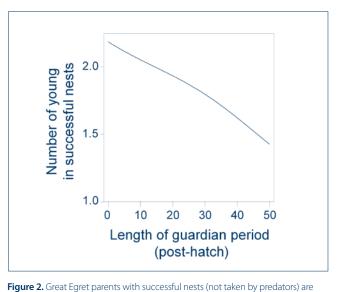


Figure 1. Average percent of Great Egret nests that escape predation in relation to the length of the nest guardian period (days after first hatch).



likely to fledge more young if they reduce the length of the nest guardian period.

2009

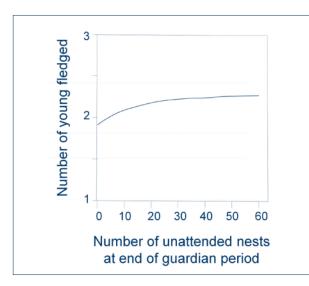


Figure 3. Great Egrets fledge more young, on average, if parents begin the postguardian period of nest attendance at a time when more nests in the colony are unattended.

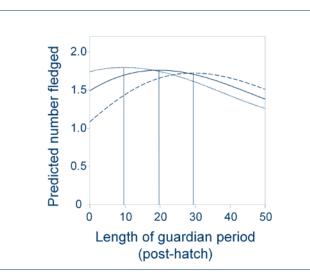


Figure 4. Predicted number of Great Egrets fledged per nest attempt at Bolinas Lagoon, plotted against the length of the nest guardian period (at average values of other variables). Dashed line = ravens present; dotted line = ravens absent; solid line = 50% chance of raven presence. Vertical reference lines indicate the predicted length of the guardian period.

ravens. We then examined the extent to which the consequences of parental behavior explained by the models were consistent with the predicted outcomes of the Dilution and Trade-off hypotheses.

Patterns of parental care

Our results were consistent with the predictions of the Trade-off Hypothesis. When egrets guarded their nests for a longer period of time, they decreased the chance of nest predation (Figure 1). However, parents that successfully avoided nest predation were likely to fledge more young if they reduced the length of the guardian period (Figure 2)—presumably because of increased time for foraging. We also found support for the Dilution Hypothesis. Great Egrets fledged more young, on average, if they began the post-guardian period when more unattended (post-guardian) nests were present in the colony (Figure 3).

Egrets that made complex decisions to optimize trade-offs in reproductive performance related to the combined risks of nest predation and nestling starvation—decisions influenced by the age of nestlings, energy demand, food supply, foraging opportunities, and predation pressure—achieved the highest reproductive success (Figure 4). How sensitive are nesting egrets to changes in predation risk and opportunities for foraging? Simulations based on our results suggested that egrets are likely respond to increases in the presence of ravens by extending the length of the guardian period, which reduces available foraging time (Figure 4). Under simulated decreases in the presence of ravens, egrets reduced the length of the guardian period, increasing foraging time.

Conservation trade-offs

Successful parenting involves complex choices based on continual assessments of multiple concerns. The most successful Great Egret parents balance the costs and benefits of guarding the nest continuously, leaving to gather food for their young, and aligning the peak period of nest vulnerability with other nests in the colony. These costs and benefits have potentially important implications for conservation.

Based on our results, restoring the quality or quantity of surrounding wetland feeding areas might not only allow nesting egrets to reduce their foraging range, spend less time foraging, or increase the amount of food they bring back to their young-it may also allow parents to increase the length of the nest guardian period. This, in turn, might allow them to compensate for increases in predation pressure related to introduced nest predators or human subsidies of ravens or other predators. Similarly, reducing the threats of introduced or subsidized nest predators in heronries might allow egret parents to reduce the length of the nest guardian period, increasing the amount of time they can spend gathering food for

their young. This, in turn, would reduce the risk of nestling starvation and help parents compensate for reduced wetland quality or quantity, including wetland losses related to climate-induced sea level rise.

If conservation efforts can protect or improve heron and egret foraging opportunities in surrounding wetlands and can limit or reduce threats caused by introduced or subsidized nest predators, then herons and egrets might be able to sustain effective levels of reproduction through adaptive parenting—in spite of dramatic changes to the environment. Alternatively, the expected result of spiraling demands on egret parents is declining colony size or abandonment of the colony site. As in other areas of conservation, the ecological implications of nesting behavior suggest benefits and concerns for the protection of heronries.

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- laying, and reproductive success in a colony of Great Blue Herons and Great Egrets. Auk 102: 49-63.

A fine scale census of herons and egrets on Bolinas Lagoon

Local Values

by Emiko Condeso

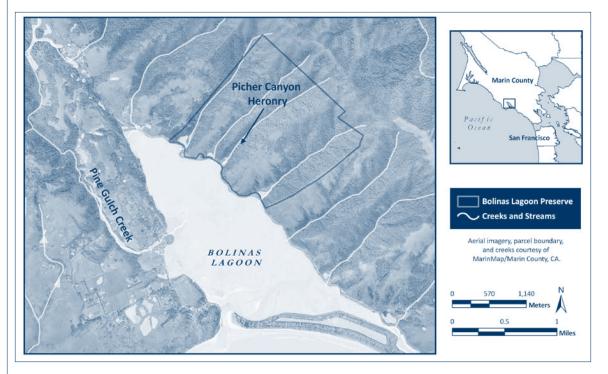
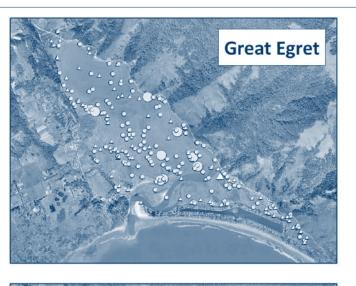


Figure 1. Bolinas Lagoon and vicinity.

In the afternoon light, the expanse of Bolinas Lagoon is a mirror whose surface is broken by exposed mudflats and rafts of floating waterbirds. The water ranges from shallow, to deep and salty, to brackish, providing a wide variety of habitats for wildlife. More often than not, herons and egrets can be seen in the shallows, foraging singly or in groups. During the breeding season, one of the largest and longest-lived heron and egret nest sites in the Bay Area can be found on the northeast shore of the lagoon at Picher Canyon, Audubon Canyon Ranch (Figure 1).

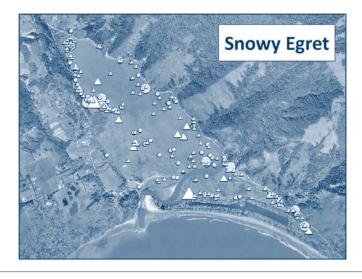
For more than 40 years, researchers at ACR have monitored the Picher Canyon heronry, using a meticulous, twice-weekly field protocol to obtain measures of colony size and reproductive success. These and other data have contributed to the recognition of Bolinas Lagoon as a wetland of international importance by the Ramsar Convention (see Ardeid 2006). Although the heronry is intensively studied, we have only just begun to examine how these birds utilize the lagoon itself. Because nesting herons and egrets tend to restrict their foraging to wetlands close to their nest sites (Kelly et al. 2008), Bolinas Lagoon is more than simply a beautiful sight—it is critical habitat upon which the reproductive success of the heronry depends.

Understanding the patterns of wading bird use of the Bolinas Lagoon will greatly enhance our ability to address local management concerns and also help to develop a more general understanding of how herons and egrets use the wetland landscape. Previous work by PRBO Conservation Science shows that numbers of herons and egrets on the lagoon have fluctuated over time (Shuford et al 1989). However, we do not yet understand the extent to which heron and egret abundance and distribution in the lagoon varies in relation to fine-scale characteristics of habitat. To address this question, and to augment a separate investigation of heron and egret foraging behavior, researchers at ACR conducted standardized censuses of Great Egrets, Great Blue Herons, and Snowy Egrets on the lagoon. From specified locations along the shore, they used binoculars and telescopes to identify the species and locations of all wading birds on the lagoon. Each one-hour census took place on a medium tide (2.5–3.5' above mean lower low water). We noted whether observed birds were solitary or in groups, whether they were in a foraging or nonforaging posture, what type of habitat they were in (emergent vegetation, upland, mudflat, etc.), and the depth of the water relative to the birds' legs. The specific location of each individual or group was recorded on an aerial photo. These data were then entered into a Geographic Information System (GIS) for analysis.









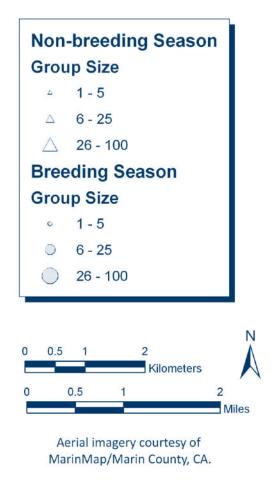
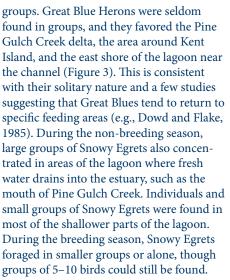


Figure 2. Distribution of herons and egrets on Bolinas Lagoon in the non-breeding (triangles) and breeding (circles) seasons (August 2005 to February 2006 and March–July 2006, respectively). The sizes of symbols represent the number of individuals in a group of foraging birds (group diameter \leq 100 m). This figure represents cumulative use of the lagoon by these species over one calendar year and does not represent the number of birds observed at any one point in time.

2009



Though extensive use of Bolinas Lagoon by herons and egrets is well known, understanding and quantifying what makes habitat in this estuary preferable is actually quite difficult. The information presented here is part of a work in progress, and areas of the lagoon with relatively little observed use may still be very important to the birds at times when they were not observed. Precisely what is needed to support healthy populations of herons and egrets is a question often asked of conservation biologists, yet supportive data are usually lacking. ACR has begun to address this question for Bolinas Lagoon, and it is our hope that future work will allow us to develop a more general understanding of these species' habitat needs. Ultimately, such information may be important in evaluating and protecting wetland quality wherever herons and egrets occur.

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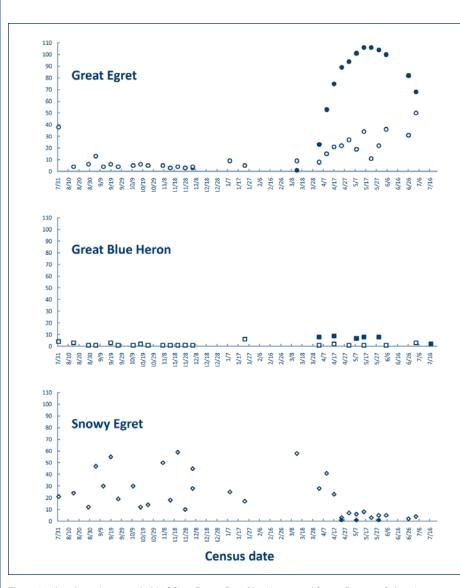


Figure 3. Abundance (open symbols) of Great Egrets, Great Blue Herons, and Snowy Egrets on Bolinas Lagoon and the number of nests (filled symbols) of each species observed at the Picher Canyon heronry, Audubon Canyon Ranch, by census date (August 2005-July 2006).

Great Egrets are a constant presence on the lagoon during the non-breeding season, typically numbering less than ten individuals at any given time (Figure 2). During the breeding season, however, the number of Great Egrets observed on the lagoon increases dramatically. This increase is consistent with the number of active nests at Picher Canyon. Great Blue Herons are not as abundant as either Great Egrets or Snowy Egrets on Bolinas Lagoon, nor do they nest in great numbers at Picher Canyon (Figure 2). Colonies of Great Blue Herons are typically small throughout the Bay Area (Kelly et al. 2006). Snowy Egrets have thus far been only occasional nesters at Picher Canyon; however, they make great use of the lagoon during the non-breeding season. During our census periods as many as 60 Snowy Egrets

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were observed on the lagoon at once (Figure 2). Snowy Egret use of the lagoon drops off sharply after the onset of the breeding season, when they are presumably tied to foraging areas closer to their breeding sites (Figure 2; Kelly, 2008).

During both the breeding and nonbreeding seasons, all species tended to congregate at creek deltas and slough margins. Great Egrets are more widely distributed throughout the lagoon than the other species observed, which may be related to their abundance and foraging behavior (Figure 3). We recorded Great Egrets in the center of the lagoon and the area south of the mouth of Pine Gulch Creek (Figure 1), places both Great Blue Herons and Snowy Egrets tended to avoid. During our study period, Great Egrets foraged individually or in small

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How seed collection influences genetic diversity in ecological restoration

Growing Diversity

by Hillary Sardiñas

Numerous creeks carve the flanks of Mount Tamalpais, in Marin County, as they snake toward the Pacific Ocean. The area's topography causes some of these streams to flow into San Francisco Bay and some directly into the Pacific Ocean, while others enter Bolinas Lagoon before reaching the sea. Although all of the creeks, including those that carved the canyons of the Bolinas Lagoon Preserve (BLP), are part of the greater Mount Tamalpais watershed, they form distinctive sub-watersheds that have different stewardship needs (Figure 1).

Each of the four canyons that comprise BLP is drained by a separate creek flowing into Bolinas Lagoon. The north- and southfacing slopes of each canyon host different species, due to numerous factors including their exposure, slope, and soil type. The north-facing slope of Volunteer Canyon is dominated by coniferous forest, whereas the canyon's south-facing slope is mostly a

mixture of oak woodland and chaparral. Between canyons, these differences become even more pronounced. For example, the California sagebrush-dominated south-facing slope in Garden Club Canyon is a dramatic contrast to the redwood forest just over the ridge in the northfacing Pike County Gulch. This varied topography is part of what allows for the incredible floristic diversity within the preserve. Yet it also provides a challenge: which plant populations ought to be the source for plants used in ACR's revegetation efforts?

Ecologists presume that, for most species, gene flow generally follows the pathways created by water, with seeds from upland populations carried downstream by gravity or rainfall events. Additionally, winds sweep up or down the canyons,

creating paths for gene flow in wind-pollinated species. However, this watershed model of gene flow does not hold true for all species. For example, fruits and berries are consumed by birds and mammals that are able to disperse seeds across watersheds and regions. Because of the diversity of mechanisms for pollination and dispersal, the concept of a "geneshed" is a useful way to view the genetic range of a plant species. Unique for every species, a geneshed can be conceptualized as the area over which a species' genetic material can successfully travel. A coconut may be able to traverse the entire Pacific Ocean, whereas a buckeye in Volunteer Canyon may only roll a few feet from its source tree. ACR's Habitat Protection and Restoration staff use the concept of genesheds to think beyond sub-watersheds when considering how far afield to roam when collecting seed for our restoration projects.

Reference sites and species selection

In 2006, Audubon Canyon Ranch started work on the Four Canyons Restoration Project—the restoration of former human-use areas to wild habitat at BLP. Our restoration sites are primarily located in canyon bottomlands and riparian floodplains, which have been affected by use as parking lots, building areas, and storage sites for equipment and materials used on the preserve. These previous disturbances made the land susceptible to invasion by weeds that compete with native plants for space, sunlight, and nutrients.

To select our planting palette, we identified reference sites with similar characteristics to our restoration site and used their species diversity to inform our project design (Figure 2). One of our goals is for our sites to re-establish habitat capable of providing abundant resources to native insect, bird, amphibian and mammal species pres-

> ent at BLP. By including ground cover, grasses, shrubs, and trees, we can ensure that there will be multiple layers of vegetation that create a variety of habitats. Incorporating plants that set seeds or produce berries enhances available food resources for wildlife. Planting insect-pollinated plants provides valuable resources for pollinators. Additionally, by using plants that vary in the timing of their seasonal reproductive cycles, from early spring annuals to woody perennials that flower in late autumn, our restoration sites will be able offer diverse resources throughout the year.

Once we have determined what species to grow for each site, seed collection can begin. Most seeds do not mature until mid-summer; they cannot be planted in the same year they are collected, because they need more time to grow to a stage

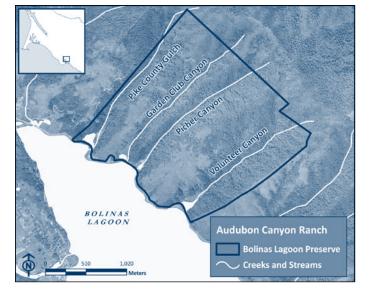


Figure 1. The creeks that created the four canyons of the Bolinas Lagoon Preserve originate on the flanks of Mt. Tamalpais and terminate in the Bolinas Lagoon. They are separated by steep ridges that isolate them from one another. For restoration purposes, we treat each canyon as its own distinct sub-watershed of Bolinas Lagoon and maintain its genetic integrity by using plants grown from seeds collected within the destination canyon.

where they have adequate resources to survive outplanting. In order to properly time a plant's readiness, collection must occur oneand-a-half years prior to the planned project, with seeds sown in pots during the spring preceding the winter planting season. Exceptions include annuals, early-maturing native grasses, and seeds that are directly sown into sites; these can be collected the spring before planting, or in the case of a late-blooming species, sown directly into sites as they mature in the late fall/early winter.

Principles of seed collection

A major concern that conservation projects confront is how to collect sufficient seed to achieve restoration goals without overharvesting from native plant populations. To address this issue, native plant nurseries have created the following three guidelines for seed collection (adapted from Young 2007, Proposed Seed Collection Guidelines, Golden Gate National Recreation Area):

1. The Five Percent Rule: Collect no more than 5% of the available seed from any species in a specific area or from any particular individual.

2. The Rule of Ten: Collect from as many plants of each species as possible throughout a collection area, and never from fewer than ten plants.

3. The Law of Space and Time: Collect throughout the species' geneshed; collect several times throughout the seed ripening period.

The Five Percent Rule is based upon findings by Menges and others at the Archbold Biological Station, Lake Placid, Florida, who stated that less intense, frequent harvests are safer than more intense, infrequent harvests. They found that high rates of seed removal (over 50%) significantly reduced population growth rate and increased probabilities of extinction in some species. By collecting only a small portion of the seeds available, we can help wild populations to persist, prosper, and provide genetic material for future projects. Additionally, at BLP we collect seeds from populations over a series of years, making sure that our efforts in a given year do not cause major demographic shifts in native plant populations.

The Rule of Ten ensures that particular versions of genes (alleles) from only a few plants do not dominate the population in restored sites (Knapp and Rice 1994; Restoration and Management Notes 12:40–45). Harvesting seed from a variety of different individuals helps to balance their genetic contributions to the population. It is for this reason that seed collectors try not to

discriminate against plants that do not appear to be as robust as other individuals. Natural populations of plants consist of a mixture of individuals that vary in size, height, and so on, due to both genetic and environmental effects. Therefore, the appearance of a plant at a particular time or place may not be a good measure of its genetic value.

The Law of Space and Time is a guideline that encourages seed collecting at several locations of the geneshed and at different times throughout a species' seed ripening season. By following this practice, collectors have a better chance of encountering early- and late-flowering varieties. Because natural populations contain plants that bloom at different intervals, this measure helps ensure that a seed sample reflects the natural variability present in the wild population. By collecting from throughout a plant's geneshed, we can increase the chances of encountering that species in different environmental conditions and of capturing adaptations associated with such variation.

All these measures help ensure that our seed inventory reflects the diversity contained within wild populations, without harming these populations. However, all these conditions beg the question: Why is diversity important?

Diversity sustains local adaptations

Genetic variation is essential because it allows populations to adapt and evolve to changing conditions. If there is not sufficient genetic variation, populations may be unable to withstand changing conditions that limit their survival or reproduction, potentially leading to extinction. Limited resources within a gene pool can lead to a condition known as inbreeding depression. Inbreeding depression can make a population vulnerable to deleterious recessive alleles-gene forms that are normally hidden or neutral in large populations but can produce dangerous traits in small populations if there is a strong likelihood of mating between genetically similar individuals (Figure 3). These traits may lower a plant's ability to survive or reproduce and can cause a small population to become extinct.

The opposite of inbreeding depression is outbreeding depression. Outbreeding depression occurs when foreign traits dilute or overwhelm local traits that evolved to





Figure 2. Restoration site (top) and associated reference site (botom) in Garden Club Canyon.

enhance survival in certain conditions. By crossing populations that have not traditionally interbred, new alleles introduced from a different environment might result in traits that decrease a plant's ability to survive or reproduce (Figure 3).

By including seeds from different locations within a local population's geneshed, seed collectors attempt to decrease the potential for inbreeding or outbreeding, while optimizing localized genetic variation. Local adaptations are important, because they may confer traits that could contribute to the resilience of native plants in restoration sites. For example, "competitive traits," such as early germination, may actually enhance growth during the seedling phase, when competition with non-native species is typically most pronounced (Leger 2008; Ecological Applications, 18:1226–1235). Because of the widespread abundance of non-native and invasive species in coastal California ecosystems, competitive traits could prove essential for the continued survival of some plants. By collecting seeds directly from a site slated to be restored and from other sites within a species' geneshed, we can ensure that localized adaptations are present.

Climate change

Although there are numerous predictions concerning the effects of climate change, none of the models reliably describe how global warming patterns will actually manifest. Collecting seeds from plants that inhabit the local extent of their geneshed (such as at different altitudes and aspects) could help protect species from climate change. For example, suppose a certain plant typically grows in shade but occasionally is found in sunny, exposed areas: by using seed from individuals growing in sunnier areas, we might be able to enhance the population's likelihood of surviving a climate shift toward drier conditions. Such crosses are risky, however, because they might lead to outbreeding depression, so a cautious approach may be critical. Therefore, the three guidelines for seed collection (above) should result in plants with varied genetic stock that are capable of establishing in the short-term and adapting to uncertain future conditions.

Even if the effects of climate change are not significant, weather and rainfall can be extremely erratic. Random natural events can have damaging effects on small, susceptible populations. For example, two

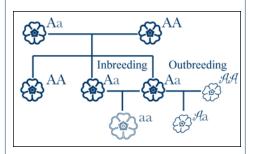


Figure 3. A represents a normal dominant version of a gene (allele), **a** represents a deleterious recessive allele, and \mathscr{H} represents a dominant allele from a foreign population. Dominant alleles typically suppress recessive alleles, however inbreeding increases the probability that recessive alleles will be expressed more frequently, which could harm the population. On the other hand, outbreeding could introduce alleles that could have beneficial *or* harmful effects, depending upon the evolutionary history of the original population.

early winters in a row could thwart the maturation of seeds and prevent a rare plant from replenishing its seed bank. If random, harmful events continue, the plant population could be threatened with extinction. By maintaining genetic diversity within restoration sites, we may promote the presence of resilient individuals to insulate the population against unpredictable weather patterns.

Toward balance

Taking all of the aforementioned factors into consideration is tricky, because we do not want to risk incorporating native plants that are not capable of surviving in our restoration sites, causing gaps that may allow invasive species to re-colonize. In order to prevent such a scenario, we monitor the survivorship of each plant species. If particular species do not survive in a site, we can replace them with different species. The information we gather enables us to measure our progress and alter any methods that are not working. This flexible and comprehensive approach favors the long-term success of our restoration sites.

Through thoughtful seed collection, careful project design that incorporates a regard for genetic diversity, and a strategy for adaptively improving our work, the Habitat Protection and Restoration team at Audubon Canyon Ranch is restoring the degraded areas at the Bolinas Lagoon Preserve. Applying the principles of diversity to our projects helps ensure that plant communities we conserve are resilient, healthy, and capable of adapting to the multiplicity of conditions the future may bring.

Visiting Investigators

Audubon Canyon Ranch hosts graduate students and visiting scientists who rely on the undisturbed, natural conditions of our sanctuaries to conduct investigations in conservation science.

Effects of invasive species on nitrogen retention and other issues in the ecology and restoration of coastal prairie. Jeff Corbin, Union College.

Carbon addition and mowing as restoration measures in a coastal California Grassland. Brody Sandel, UC Berkeley.

Ecological indicators in West Coast estuaries. Steven Morgan, Susan Anderson, and others, Pacific Estuarine Ecosystem Indicator Research (PEEIR) Consortium [www-bml. ucdavis.edu/peeir].

Long-term monitoring of the Giacomini wetland. Lorraine Parsons, Point Reyes National Seashore.

Analysis of sedimentation in natural and restored marshes. Lorraine Parsons, Point Reyes National Seashore.

Factors causing summer mortality in Pacific oysters. Fred Griffin, UC Davis Bodega Marine Lab.

A comparison of carbon cycling and material exchange in grasslands dominated by native and exotic grasses in northern California. Laurie Koteen, UC Berkeley. *Black Brant counts at Drakes Estero, Tomales Bay and Bodega Bay.* Rod Hug, Santa Rosa, California.

Strophariaceae of California. Peter Werner, Dennis Desjardin, San Francisco State University.

Effects of landscape context and recreational use on carnivores in northern California. Sara Reed, UC Berkeley.

Impact of an introduced plant pathogen on Lyme disease ecology. Cheryl Briggs and Andrew Swei, UC Berkeley.

Impacts of Wild Turkey (Maleagris galpavo) *on native avifauna in northern California*. Angela Gillingham, Duke University/California State Parks.

Effects of planktivorous fish predation on larvae release patterns of estuarine crabs. Leif Rasmuson, University of Puget Sound.

Investigtion of fossil Olivella (a marine snail) from the Millerton Formation at Toms Point, Tomales Bay. Daniel Muhs, U.S. Geological Survey. A camera trap survey of mammals and birds at Audubon Canyon Ranch, Rich Tenaza, University of the Pacific, and Chris Wemmer, California Academy of Sciences.

Non-fire and non-soil controls of the chaparral/ grass boundary in California. Marc Coudel, UC Davis.

Field verification of habitat connectivity models for the Mayacamas Mountains ecosystem. Justin Kitzes, Sarah Reed, and Adina Merenlender, UC Berkeley.

Initial Suyrvey of vegetation used for questing by Ixodes pacificus (Acri: Ixodidae). Martin Castro, California Department of Health Services, Vector-borne Disease Section.

Tidewater goby assessment and protection activities associated with the Giacomini Ranch Restoration Project. Darren Fong, Golden Gate National Recreation Areas.

In Progress: project updates

Current projects by Audubon Canyon Ranch focus on the stewardship of sanctuaries, ecological restoration, and issues in conservation science.

Picher Canyon Heron and Egret Project D The fates of all nesting attempts at ACR's Picher Canyon heronry have been monitored annually since 1967, to track long-term variation in nesting behavior and

Tomales Bay Shorebird

reproduction.

Project D Since 1989, we have conducted annual shorebird censuses on Tomales Bay. Each census involves six baywide winter counts and one baywide count each in August and April migration periods. A team of 15–20 volunteer field observers is needed to conduct each count. The data are used to investigate winter population patterns, local habitat values, and implications for shorebird conservation.



A Natural Resources Management Plan for Modini Ingalls Ecological Preserve

Audubon Canyon Ranch has signed a collaborative, planned giving agreement with Jim and Shirley Modini to acquire 1,725 acres in northern Sonoma County. The property, to be known as the Modini Ingalls Ecological Preserve, has been in the Modini Ingalls family since 1867. This remote, undisturbed landscape is a rich blend of oak woodlands, pine forests, perennial grasslands, chaparral, serpentine outcrops, and wild streams. Sherry Adams is developing a comprehensive plan for long-term stewardship, including field surveys to assess biological values, cultural history, and management needs. The work is being made possible through generous support provided by Jim and Shirley Modini. The completed plan will include implications for regional conservation in the central Mayacamas Mountains (see photo on back cover).

Tomales Bay Waterbird

Survey Since the winter of 1989–90, teams of observers have conducted winter waterbird censuses from survey boats on Tomales Bay. The results provide information on habitat values and conservation needs of more than 50 species. We are currently investigating trends in species abundances and relationships with Pacific herring roe as important food for wintering waterbirds in Tomales Bay.

North Bay Counties Heron

and Egret Project
Annual monitoring of reproductive activities at all known heron and egret nesting colonies in five northern Bay Area counties began in 1990. We are currently investigating the effects of landscape habitat patterns on nesting herons and egrets. ACR's 250-page Annotated Atlas and Implications for the Conservation of Heron and Egret Nesting Colonies in the San Francisco Bay Area includes an analysis of the regional status and trends of herons and egrets and provides individual accounts of all known heronries in the area (www. egret.org/atlas.html). We have also developed a reference that uses Google Earth to show the locations and status of northern Bay Area heronries (www.egret. org/googleearth2.html).

Impacts of Wild Turkeys on Forest Ecosystems Dan

Gluesenkamp is conducting a study to experimentally measure the effects of ground foraging by invasive, non-native Wild Turkeys on vegetation and invertebrates in the forest ecosystem of Bouverie Preserve.

Four Canyons Project ACR's

Bolinas Lagoon Preserve contains four canyons that drain the western slope of Bolinas Ridge. We are restoring the natural complexity of native vegetation in the lower reaches of these canyons, repairing disturbed sites, and eradicating or controlling invasive plant species. Native plant propagation facilities in Volunteer Canyon are being used to grow locally collected plant materials for restoration.

Monitoring and Control of Non-Native Crayfish

Jeanne Wirka and others are studying the distribution of non-native signal crayfish (Pacifastucus lenisculus) in Stuart Creek at Bouverie Preserve and investigating the use of barriers and traps to control the potential impacts of crayfish on native amphibians and other species.

Highway-Generated Nitrogen Deposition in Vernal Wetlands

▶ Enhanced availability of nitrogen near highways might facilitate invasion by non-native plant species in sensitive vernal wetlands. Dan Gluesenkamp, Stuart Weiss, and Jeanne Wirka are quantifying the potential effects of highway-generated nitrogen deposition on Sonoma Valley vernal pools.

Plant Species Inventory

Resident biologists maintain inventories of plant species known to occur on ACR's Tomales Bay properties and at Bouverie and Bolinas Lagoon preserves.

Annual Surveys and Removal of Non-Native Spartina and

Hybrids ▶ In collaboration with the San Francisco Estuary Invasive Spartina Project, Emiko Condeso and Gwen Heistand coordinate and conduct comprehensive field surveys for invasive, non-native *Spartina* in the shoreline marshes of Tomales Bay and Bolinas Lagoon.

Monitoring and Eradication of Perennial Pepperweed in

Tomales Bay ▶ Invasive, nonnative pepperweed (*Lepidium latifolium*) is known to quickly cover floodplains and estuarine wetlands, compete with native species, and alter habitat values. We are using a variety of methods to remove and monitor the first known infestations in Tomales Bay and, hopefully, prevent further invasion.

Saltmarsh Ice Plant Removal

We have eradicated nonnative ice plant from marshes and upland edges at Toms Point on Tomales Bay, although management to remove resprouts and new patches continues. Native vegetation has recruited into areas where ice plant was once dominant.

Eradication of *Elytrigia* pontica ssp. pontica > *Elytrigia*

is an invasive, non-native perennial grass that forms dense populations in seasonal wetlands. At Bouverie Preserve, we are eliminating a patch of *Elytrigia* using manual removal, light starvation/solarization (black plastic tarps), and herbicide spot treatments of outlier patches.

Nest Boxes Dony Gilbert maintains Western Bluebird nest boxes in the Cypress Grove grasslands. Rich Stallcup maintains several Wood Duck nest boxes along Bear Valley Creek in ACR's Olema Marsh.

Restoration of Coastal Dunes by Removal of *Ammophila*

arenaria Ammophila arenaria is a highly invasive, non-native plant that alters the topography and function of coastal dunes. Removal of Ammophila at Toms Point, on Tomales Bay, is helping to protect native species that depend on mobile dune ecosystems.

Vernal Pool Restoration and Reintroduction of Imperiled

Plants Dan Gluesenkamp, Jeanne Wirka, and Sherry Adams are restoring habitat conditions in the vernal pools at Bouverie Preserve. The project includes the removal of invasive plants and re-establishment of the federally listed Sonoma sunshine (Blennosperma bakeri) and California species of conservation concern dwarf downingia (Downingia pusilla). The work involves manual effort by volunteers, propagation and planting of native plants, use of prescribed fire, cattle grazing, and monitoring of vegetation and hydrology.





Ardeid (Ar-DEE-id), N., refers to any member of the family Ardeidae, which includes herons, egrets, and bitterns.

The Ardeid is published annually by Audubon Canyon Ranch as an offering to Conservation Science and Habitat Protection field observers, volunteers, and supporters. To learn more about this program and how to support Audubon Canyon Ranch, please contact the Cypress Grove Research Center (cgrc@egret.org or 415.663.8203) or ACR's headquarters (acr@egret.org or 415.868.9244). ©2009 Audubon Canyon Ranch. Printed on recycled paper. Managing Editor, John Kelly. Layout design by Claire Peaslee. I www.egret.org

Conservation Science and Habitat Protection at Audubon Canyon Ranch

AUDUBON CANYON RANCH—A SYSTEM OF WILDLIFE SANCTUARIES AND CENTERS FOR NATURE EDUCATION.

BOLINAS LAGOON PRESERVE • CYPRESS GROVE RESEARCH CENTER • BOUVERIE PRESERVE

Southward view across the Modini Ranch in the Mayacamas Mountains of northern Sonoma County.



anne Wirka / AC

Long-term stewardship plan see page 13



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