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Original Article

Caspian Tern Response to Managed Reductions in Nesting Habitat

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ABSTRACT Predation on smolts by Caspian terns (*Hydroprogne caspia*) has been identified as a factor limiting the restoration of some populations of anadromous salmonids (*Oncorhynchus* spp.) from the Columbia River basin that are listed under the U.S. Endangered Species Act. Implementation of a management plan to reduce numbers of Caspian terns nesting at the 2 largest colonies in the Columbia Plateau region of Oregon and Washington, USA, began in 2014 and is ongoing. We investigated the response of Caspian terns during 2014–2016 to reductions in nesting habitat at these 2 colonies. Management prevented terns from nesting at both colonies, and the estimated numbers of nesting pairs in the region declined significantly from a mean of 877 pairs during premanagement to 769 and 675 pairs in 2015 and 2016, respectively. The management objective of reducing numbers of nesting terns in the Columbia Plateau region to ≤200 breeding pairs was not achieved during the first 2 years of full implementation of the plan. Regional nesting success did not decline significantly following the initiation of management, and remained at levels considered sufficient to sustain the regional subpopulation. Despite the species' capacity for long-distance breeding dispersal, the majority of displaced terns exhibited stronger than expected philopatry to the Columbia Plateau region. Analysis of resightings of banded terns indicated that most (>80%) terns that nested in the Columbia Plateau region premanagement returned to the region in 2015 and 2016, but the proportion that returned as breeders decreased while the proportion that returned as nonbreeding floaters increased compared with premanagement. The proportion of banded terns that were unobserved also increased during management years, suggesting that more terns became floaters in the Pacific Flyway and went unobserved because they were prospecting and foraging in locations or regions where there was little or no monitoring. The unexpectedly high regional philopatry exhibited by terns during management was likely a reflection of the low availability of suitable alternative nesting habitat outside the region. Most terns that remained in the region displayed considerable flexibility in nest site selection by nesting either at a previously smaller, intermittently successful breeding colony or at a small new colony where nesting activity had not previously been recorded. As long-lived seabirds, Caspian terns may integrate information regarding nesting success over several years before choosing to change nesting locations, longer than the 2 years of this study, especially if alternate locations are distant or intermittently available, or a history of nesting at multiple locations exists within the region.

KEY WORDS avian predation, Columbia Plateau, habitat loss, *Hydroprogne caspia*, salmonid restoration, salmonids.

Conflict between fisheries and piscivorous wildlife that consume anadromous salmonids (*Oncorhynchus* spp.) in the Columbia River basin has persisted for decades (Ruggerone 1986, Steuber et al. 1995, York et al. 2000). This conflict became more prominent following the listing of 13 of the 20 populations of salmonids in the Columbia River basin as threatened or endangered under the U.S. Endangered Species Act (ESA 1973, as amended; Good et al. 2007). Avian predators on juvenile salmonids have been identified as a limiting factor in the restoration process for Columbia River basin salmonids (Evans et al. 2012, USACE 2014). In particular, Caspian terns (*Hydroprogne caspia*) nesting at a large colony in the Columbia River estuary consumed an estimated 8.1 million juvenile salmonids in 1997 and 12.4 million juvenile salmonids in 1998

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(Roby et al. 2003), which corresponded to a significant proportion of several listed populations (Collis et al. 2001).

The North American Pacific Flyway population of Caspian terns has increased dramatically since 1960 (Suryan et al. 2004). Although the Caspian tern colonies in the Columbia Plateau region of eastern Washington, USA, are far smaller than the large colony in the Columbia River estuary, the estimated per capita consumption rate of juvenile salmonids by terns nesting at the largest colony in the Columbia Plateau region (Crescent Island) was far higher than that of terns nesting in the Columbia River estuary (Evans et al. 2012).

Caspian terns that nest in the Columbia Plateau region have been identified as a limiting factor for restoration of certain listed populations of anadromous salmonids that originate from the Upper Columbia and Snake River basins. The Inland Avian Predation Management Plan (IAPMP) was developed by the Inland Avian Predation Working Group, an interagency working group led by the U.S. Army Corps of Engineers (USACE), in order to reduce the losses of juvenile salmonids due to avian predation. The IAPMP called for the elimination of Caspian tern nesting habitat at the 2 largest colony locations in the Columbia Plateau region: Crescent Island in McNary Reservoir on the Columbia River near Pasco, Washington, and Goose Island in Potholes Reservoir near Moses Lake, Washington (USACE 2014).

It has been repeatedly demonstrated that Caspian terns can locate and colonize newly formed nesting habitat within a single nesting season (Sirdevan and Quinn 1997, Roby et al. 2002, Suzuki 2012). Caspian terns breeding in the Pacific Flyway have exhibited high connectivity among colony sites (Suzuki 2012). Some individuals in the Pacific Flyway population have exhibited long-distance breeding dispersal (>3,000 km), and there is high connectivity between colonies on the Pacific Coast and inland colonies in the Columbia Plateau region (Suzuki 2012). Long-distance natal and breeding site dispersal has been documented for Caspian terns and other tern species, but the rates of long-distance dispersal have been consistently low and most individuals display high breeding-site fidelity (Suzuki 2012). Väisänen (1973) documented a colony-deserting flight, however, resulting in a Caspian tern colony in the Baltic Sea relocating 800 km away following regular human disturbance. Now that the nesting habitat formerly used by the majority of breeding Caspian terns in the Columbia Plateau region is unavailable, there may not be sufficient habitat for all terns that are motivated to nest in the region, potentially resulting in increasing rates of long-distance breeding dispersal, or a shift to marginal nesting habitat in the Plateau region that can only support low nesting-success rates.

The numbers of Caspian terns nesting in the Columbia Plateau region more than doubled from 1980 to 2000 (Shuford and Craig 2002, Suryan et al. 2004). The increase in the subpopulation occurred in conjunction with anthropogenic habitat alterations (Wires and Cuthbert 2000, Collis et al. 2001). Crescent Island in McNary Reservoir on the Columbia River was constructed of dredged material in the mid-1980s, and Goose Island was created by the construction of O'Sullivan Dam, which formed Potholes Reservoir in 1951. Thus, the 2 islands that supported the 2 largest Caspian tern breeding colonies in the Columbia Plateau region were anthropogenic in origin. Both islands offered secure, unvegetated nesting habitat for Caspian terns that was not subject to inundation resulting from wide fluctuations in reservoir levels, and not subject to vegetation encroachment due to rocky soils, arid regional climate, and isolation from the underlying water table. Historically, Caspian terns have nested mostly in highly ephemeral natural habitats (Wires and Cuthbert 2000, Collis et al. 2001), such as low-lying sandy islands subject to periodic erosion and accretion.

In addition to the 2 main colonies at Crescent Island and Goose Island, Caspian terns regularly nested at 3 or 4 other sites scattered across the region, where small colonies (<100 average breeding pairs) existed prior to the initiation of management under the IAPMP (Adkins et al. 2014). If Caspian terns displaced from colonies on Crescent and Goose islands disperse to other prospective colony sites within the Columbia Plateau region, they may settle at more ephemeral locations, such as low-lying gravel-bars or sandbars, where nesting habitat and nesting success would likely be limited. Alternatively, the motivation of terns to find suitable nesting sites and reproduce may drive them to search outside the Columbia Plateau region and find newly available habitat far from the Columbia River basin and its salmonid runs. The USACE constructed alternative tern nesting habitat in San Francisco Bay (~1,000 km from the Columbia Plateau region), in part to compensate for the loss of nesting habitat in the Columbia Plateau region as part of the overall plan to redistribute Caspian terns away from the Columbia River Basin to other locations within the Pacific Flyway (USACE 2014).

Caspian terns displaced from the colony sites at Crescent and Goose islands might be expected to emigrate to either 1) other smaller extant colonies nearby, causing an increase in colony size; 2) former colony sites nearby that have not supported breeding colonies for 5–25 years; 3) new colony sites nearby with no documented history of nesting; or 4) colony sites outside the Columbia Plateau region. If displaced Caspian terns were to simply shift to other colony locations within the Columbia Plateau region instead of dispersing outside the region, the goal of the IAPMP to reduce tern predation on juvenile salmonids in the Columbia Plateau region would not be met, and the intended benefits to salmonid populations of reduced tern predation could be limited. To determine the extent to which the IAPMP was successful at reducing Caspian tern predation on juvenile salmonids in the Columbia Plateau region, it is necessary to evaluate the response of Caspian terns to the loss of nesting habitat at Crescent and Goose islands.

To evaluate the response of terns to implementation of the IAPMP, we tested the hypotheses that a managed reduction in Caspian tern nesting habitat will 1) reduce the number of Caspian terns breeding within the Columbia Plateau region, 2) reduce the reproductive success of Caspian terns breeding

within the Columbia Plateau region, and 3) result in an increase in emigration of Caspian terns from the Columbia Plateau region to colonies outside of the region. We reasoned that if managed elimination of nesting habitat at the 2 largest breeding colonies for Caspian terns in the Columbia Plateau region were successful, breeding Caspian terns would be forced to find nesting habitat outside of the region, and/or utilize more ephemeral habitat that could significantly reduce their average reproductive success.

STUDY AREA

We conducted our study in the Columbia Plateau region of central Washington State and north-central Oregon, USA (Fig. 1). The study area included the reservoirs and free-flowing reaches of the mid-Columbia River from Chief Joseph Dam (in Bridgeport, WA, below the Grand Coulee Dam) downstream to The Dalles Dam (near The Dalles, OR), the lower Snake River from Lewiston, Idaho, to its confluence with the Columbia River, other large tributaries of the Columbia River (e.g., the Yakima River), Potholes Reservoir in Grant County, Washington, and multiple other lakes and reservoirs in central Washington. The region is semiarid with limited topographic relief and dominated by sagebrush–steppe habitat and agricultural uses that are supported by irrigation. Prior to the initiation of management, the majority of breeding Caspian terns in the Columbia Plateau region nested on either Goose Island (46°59′08.67″N, 119°18′38.52″W) or Crescent Island (46°05′36.12″N, 118°55′52.14″W). Both islands were also home to much larger breeding colonies of California gulls (*Larus californicus*) and ring-billed gulls (*L. delawarensis*).

In addition, smaller colonies of Caspian terns occurred throughout the Columbia Plateau region. The Blalock Islands (45°53′43.06″N, 119°38′51.46″W) form a small archipelago in the John Day Reservoir in the Columbia River just upstream from Boardman, Oregon, and were occupied by nesting terns prior to the initiation of management. Harper Island (47°14′52.08″N, 118°05′05.19″W) is located in Sprague Lake, a small lake northeast of Crescent Island and Goose Island and home to larger colonies of breeding California gulls, ring-billed gulls, and double-crested cormorants (*Phalacrocorax auritus*). Twinning Island (47°37′29.86″N, 119°18′11.35″W) lies in the southern portion of Banks Lake near Coulee City, Washington, and

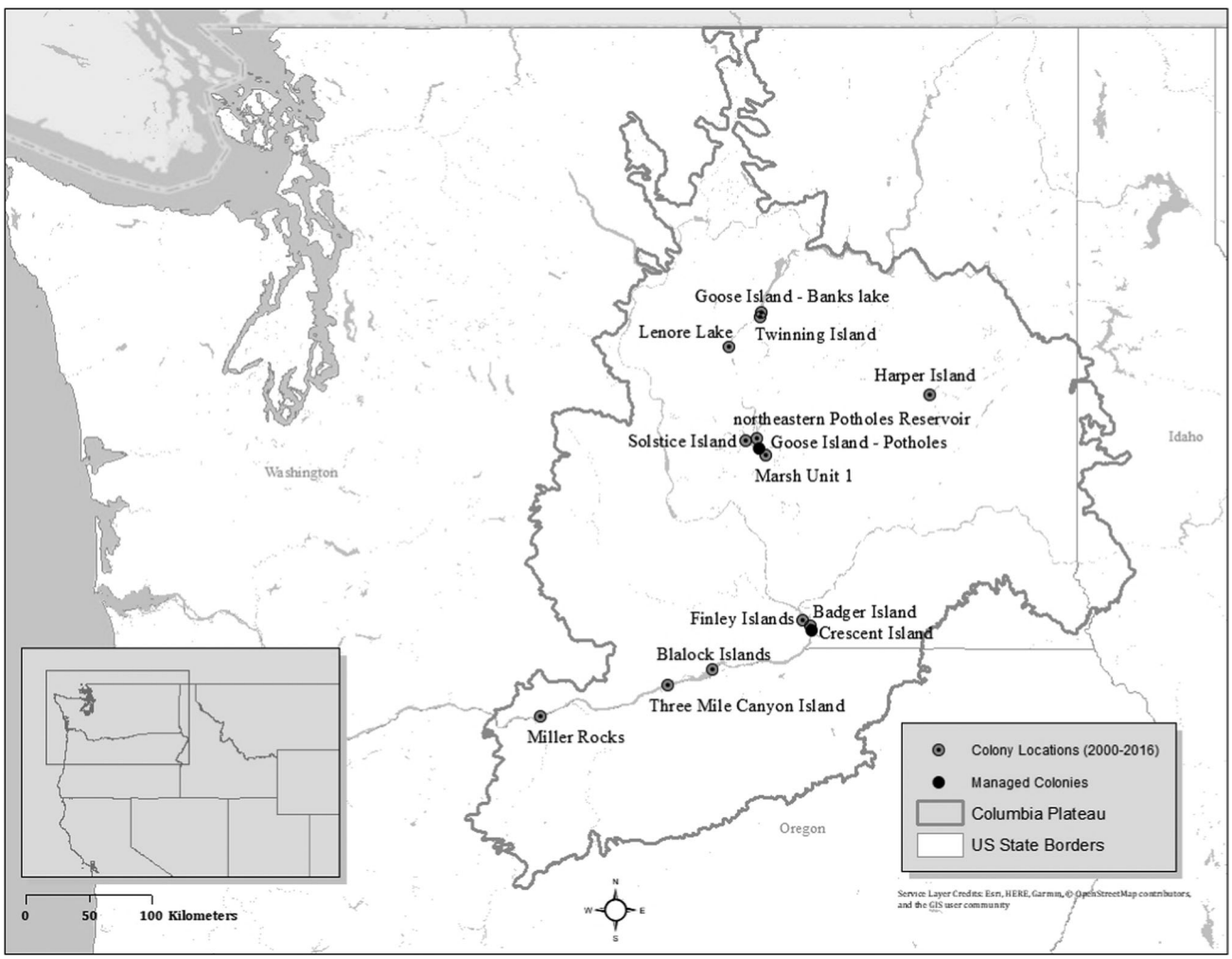

Figure 1. Map of Columbia Plateau region of Oregon and Washington, USA, showing the location of Goose Island in Potholes Reservoir and Crescent Island in McNary Reservoir, as well as the location of other Caspian tern breeding colonies in the Columbia Plateau region, during management at Goose and Crescent islands.

is also home to larger colonies of California gulls and ring-billed gulls. These locations were all used by nesting Caspian terns during the year prior to the initiation of management in the Columbia Plateau region. North Potholes reservoir (47°02′03.50″N, 119°19′37.16″W) is a maze of canals and small, low-lying sand islets where terns had nested until 2003 at a location dubbed Solstice Island (Antolos et al. 2004). Lenore Lake (47°28′48.38″N, 119°31′26.13″W) lies just south of Banks Lake where terns began nesting after the initiation of management on a small rocky island already occupied by breeding ring-billed gulls, a small number of California gulls, and double-crested cormorants.

METHODS

Summary of Management at Goose and Crescent Islands

With the objective of reducing Caspian tern breeding colonies to <40 pairs on each island, we implemented management to reduce availability of nesting habitat at Goose Island beginning in 2014, and at Crescent Island beginning in 2015 (USACE 2014). We deployed passive nest dissuasion materials, consisting of a dense network of stakes, ropes, and flagging, on all suitable tern nesting habitat on both islands. At Crescent Island only, we also deployed fence rows of privacy fabric and brush piles of woody debris in suitable habitat. We installed passive dissuasion materials over formerly used tern nesting habitat, as well as marginal nesting habitat that terns might use on either island. We also made efforts to dissuade the large colonies of California and ring-billed gulls from nesting on the islands, based on the assumption that persistence of these colonies would attract Caspian terns to continue to nest at these locations. Once terns and gulls began arriving to initiate nesting at Goose and Crescent islands, personnel stationed on the islands actively hazed the prospecting adults (Roby et al. 2014, 2015, 2016).

Surveys for Incipient Caspian Tern Colonies

We conducted boat-based and ground-based surveys of historical Caspian tern colony sites and previously identified potential colony sites weekly throughout the Columbia Plateau region during the 2015 and 2016 breeding seasons. Surveys were further guided by periodic aerial surveys using fixed-wing aircraft that surveyed historical, current, and potential nesting habitat on a predetermined flight path. Ground-based and boat-based surveys for active Caspian tern breeding colonies were also guided by the reported locations of Caspian terns that were tagged with PTT satellite transmitters prior to the 2014 and 2015 breeding seasons on either Goose Island or Crescent Island; most of these tagged terns were present in the region during the 2015 and 2016 breeding seasons (D. E. Lyons et al., Oregon State University, unpublished data).

Monitoring at Active Caspian Tern Colonies

We visited active Caspian tern breeding colonies in the region at least twice per week during the 2015 and 2016 breeding seasons, and observed them from semipermanent or pop-up blinds, when possible. We visited large, active Caspian tern colonies (>100 nesting pairs) ≥3 times/week during the breeding season and observed them from semipermanent observation blinds near the colony. We collected data visually from blinds during colony visits, including colony attendance (numbers of adult terns present), numbers of active tern nests, numbers of tern chicks present, nesting chronology, resightings of banded terns, and factors limiting nesting success.

Regional Population Size and Nesting Success

We used high-resolution aerial photography during late May (i.e., peak incubation) to count incubating birds present at each colony. We used vertical photography for colonies that appeared to have >30 breeding pairs and oblique photography for those that appeared to have <30 pairs. We determined maximum size of each colony from aerial images or ground surveys, whichever count was greater. We then summed the peak counts for each colony to estimate the number of breeding pairs in the Columbia Plateau region for each year. We estimated regional nesting success (i.e., mean no. of young raised per pair) as the sum of the maximum count of chicks from ground surveys at each colony 7–10 days after the first fledgling was observed, divided by our estimate of total breeding pairs (Patterson 2012). We used linear regression to test for trends in regional population size and nesting success.

We acquired historical data on number of nesting pairs and nesting success of Caspian terns in the Columbia Plateau region from Antolos et al. (2004), Adkins et al. (2014), unpublished annual reports during 2000–2013 (http://www.birdresearchnw.org), and C. J. Maranto (University of Washington, personal communication). For some early years during the premanagement period there was limited information collected regarding the number of fledglings produced at some smaller tern breeding colonies. In those years, we did not include colony sizes for colonies without nesting success data in the calculation of overall nest success. However, we did include the colonies with limited information on nesting success in the estimate of total number of Caspian tern nesting pairs.

We compared regional numbers of Caspian tern nesting pairs and regional tern nesting success after the full implementation of the IAPMP (2015 and 2016) each to the historical average (2000–2013) using one-sample *t*-tests. We did not include data on breeding abundance and nest success from 2014 in this analysis because the management treatments were underway but not completed (Goose Island) and not yet started (Crescent Island) during the 2014 breeding season, which likely affected the breeding colonies differently during that year.

Dispersal

During the 2005–2011 breeding seasons, we captured large numbers of adult Caspian terns ($n = 775$) and fledgling Caspian terns ($n = 3{,}344$) and fitted them with standard metal leg bands and field-readable leg bands with a unique alphanumeric code at breeding colonies within the study

area and at other colony locations throughout the Pacific Flyway, including colonies in California, Oregon, Washington, and Alaska (Y. Suzuki, unpublished data). Of these, we banded 146 adults and 667 chicks at the Crescent Island colony and 110 adults and 288 chicks at the Goose Island colony. We collected resighting data for banded Caspian terns during the 2014–2016 breeding seasons throughout the Columbia Plateau region during each survey or monitoring session, where feasible. Any adult Caspian tern banded with a field-readable leg band that was observed at a given colony site was recorded and its breeding status assessed. We made all band resighting observations within 60 m of the edge of a colony. We searched at larger colonies (>200 nesting pairs) for banded individuals more intensively than at smaller colonies, per a standard resighting protocol. We used these observations to monitor philopatry and dispersal from the breeding colony where each tern was banded.

We used the data set of resightings of banded Caspian terns in the Pacific Flyway (Y. Suzuki, unpublished data) to identify a subset of banded terns that exhibited a history of nesting (colony attendance) at either the Goose Island colony or the Crescent Island colony, prior to the initiation of management under the IAPMP. We defined banded terns as Breeders at one of these colonies premanagement if we resighted the individual ≥5 times over a period of ≥3 weeks and/or confirmed breeding status because we observed the banded individual either incubating eggs, brooding nestlings, or attending–feeding chicks. These criteria for the Breeder designation avoided including terns that were only resighted at a colony during a short period; we classified such birds as Nonbreeders for that season. Furthermore, we classified banded birds that were resighted within the Columbia Plateau region during a breeding season as either a Plateau Breeder or a Plateau Nonbreeder during that season. We defined banded birds that were observed at colonies outside of the Columbia Plateau region as either an Off-Plateau Breeder or an Off-Plateau Nonbreeder during that season, based on the same criteria. Finally, we considered banded birds that were not resighted anywhere during a given breeding season as having Unknown status for that season.

We used these definitions to investigate transitions between consecutive breeding seasons in the breeding status of banded individuals. The high degree of connectivity among Caspian tern colonies in the Pacific Flyway (Suzuki 2012; Y. Suzuki, unpublished data) is reflected in movement of banded individuals among colonies and regional subpopulations, as well as banded birds that may shift between breeding and nonbreeding status, depending on an individual's physiological condition or opportunities for breeding (Dobson and Jouventin 2010, Giudici et al. 2010). Therefore, we used data collected on changes in the breeding status of banded individuals between consecutive years to determine whether these background rates of intercolony movement and shifts in breeding status changed significantly following implementation of the IAPMP.

We included individual banded terns in this analysis based on whether they were classified as Plateau Breeders at either the Goose Island colony in 2013 or the Crescent Island colony in 2014, the last years before implementation of management at each respective colony. We compiled transitions between consecutive years in breeding status for this sample of banded terns from 2011 to 2016. We were particularly interested in whether implementation of the IAPMP resulted in elevated dispersal away from the Columbia Plateau region or shifts from Breeder status to Nonbreeder status within the region. Hence, we focused on whether transitions from Plateau Breeder to either Plateau Nonbreeder, Off-Plateau Breeder, Off-Plateau Nonbreeder, or Unknown increased following the implementation of management. The implementation of management could induce terns to transition to nonbreeder status before emigrating from the Columbia Plateau region, so we also focused on whether transitions from Plateau Nonbreeder to either Off-Plateau Breeder, Off-Plateau Nonbreeder, or Unknown increased following the implementation of management.

We used Fisher's exact test to test the hypothesis that the change in proportions for each transition (breeding state and/or location change; e.g., Plateau Breeder-Plateau Nonbreeder) between consecutive years during management (2014–2015 and 2015–2016) were different from combined transitions premanagement (2011–2012, 2012–2013). This was followed by a post hoc comparison using a 2×2 contingency table. We compared the proportion of each transition versus the sum of all other transitions within each statistically significant transition year (2 consecutive years that encompass a single transition; e.g., 2014–2015) during management with the same proportion premanagement. There are 5 different transition types within each year of the post hoc analysis; therefore, we utilized a Bonferroni correction of 0.01 (α-level of 0.05/5 comparisons) as the significance threshold. We excluded the 2013–2014 transition from this analysis because management was implemented only at Goose Island in 2014, plus the individual banded terns included in the analysis were selected based on their breeding status at Goose Island in 2013 or at Crescent Island in 2014, potentially confounding the 2013–2014 transition results.

We performed this study using protocols for animal care and use (ACUP #4567) that were approved by the Institutional Animal Care and Use Committee at Oregon State University.

RESULTS

Premanagement (2000–2013), 82% of the 877 Caspian tern breeding pairs that nested in the Columbia Plateau region did so at either Goose Island or Crescent Island (Table 1). Consequently, the average nesting success during 2000–2013 of Caspian terns in the Columbia Plateau region (0.39 young fledged/breeding pair) largely reflected the average nesting success at these 2 colonies (Table 2). Management to reduce the size of the Caspian tern colony on Goose Island was initiated in 2014 and was successful at

Table 1. Number of nesting pairs at each Caspian tern breeding colony in the Columbia Plateau region of Oregon and Washington, USA, during the 2000–2016 study period. Data on number of nesting pairs from 2014 were not included in comparisons between premanagement (2000–2013) and during management (2015–2016).

Location	Historical average (2000–2013)	2014	2015	2016
Crescent Island, McNary Reservoir[a]	467	474	0	0
Goose Island, Potholes Reservoir[a]	253	156	2	0
Blalock Islands, John Day Reservoir	38	45	677	483
Twinning Island, Banks Lake	17	67	64	6
Harper Island, Sprague Lake	8	8	10	3
Lenore Lake	0	2	16	39
Northeastern Potholes Reservoir	0	0	0	144
Finley Islands, McNary Reservoir	0	0	1[b]	0
Marsh Unit 1, Columbia National Wildlife Refuge	0	0	2[b]	0
Solstice Island, Potholes Reservoir	61	0	0	0
Three Mile Canyon Island, John Day Reservoir	19	0	0	0
Miller Rocks, The Dalles Reservoir	1	0	0	0
Badger Island, McNary Reservoir	6	0	0	0
Goose Island, Banks Lake	7	0	0	0
Totals	877	752	772	675

[a] Breeding colonies where management occurred.
[b] Not included in final totals for analysis.

reducing the size of the colony to 156 breeding pairs from 340 breeding pairs the year before. Despite the reduction in numbers of Caspian terns nesting on Goose Island, no major shifts in the numbers of nesting pairs or their distribution occurred within the Columbia Plateau region during 2014 (Table 1); however, 2 pairs of Caspian terns attempted to nest for the first time on a small island in Lenore Lake (Fig. 1).

In 2015, management to reduce Caspian tern nesting habitat expanded to include Crescent Island. Management at Goose Island and Crescent Island was successful in meeting the management objective of reducing colony size to less <40 nesting pairs on each island. Only 2 pairs of Caspian terns fledged chicks from Goose Island in 2015. The Blalock Islands colony grew from 45 nesting pairs in 2014 to 677 nesting pairs in 2015. The Lenore Lake colony grew from 2 breeding pairs in 2014 to 16 breeding pairs in 2015. Nesting success at this location increased from no success in 2014 to 0.38 fledglings/breeding pair in 2015 (Table 2). The numbers of breeding pairs at other small colonies in the region remained similar to historical averages (Table 1).

In 2015, small numbers of Caspian terns briefly attempted to nest at 2 other previously unoccupied locations. Terns were often observed loafing at the Finley Islands (46°08′35.97″N, 118°59′35.97″W; Fig. 1). A Caspian tern egg was discovered on one of the islands on 18 April, but the site was abandoned shortly thereafter. Caspian terns were also discovered loafing on Marsh Unit 1 (46°57′17.21″N, 119°15′43.06″W; Fig. 1). Two active tern nests with eggs were observed in early May but failed shortly thereafter. Neither of these locations was occupied by nesting terns in 2016. Nesting attempts at the Finley Islands and Marsh Unit 1 were brief and were not included in our analyses because failure occurred well before the peak of nesting in the region.

In 2016, management was successful at completely preventing Caspian terns from nesting at both Goose and

Table 2. Nesting success (average number of young fledged per breeding pair) at each Caspian tern breeding colony in the Columbia Plateau region during the 2000–2016 study period. "—" indicates that no Caspian terns nested at that colony site in that year. Data on nesting success from 2014 were not included in comparisons between premanagement (2000–2013) and during management (2015–2016).

Location	Historical average (2000–2013)	2014	2015	2016
Crescent Island, McNary Reservoir*	0.43	0.33	—	—
Goose Island, Potholes Reservoir*	0.38	0.29	1.00	—
Blalock Islands, John Day Reservoir	0.12	0.33	0.36	0.43
Twinning Island, Banks Lake	0.00	0.00	0.00	0.00
Harper Island, Sprague Lake	0.00	0.00	0.00	0.00
Lenore Lake	—	0.00	0.38	0.59
Northeastern Potholes Reservoir	—	—	—	0.00
Finley Islands, McNary Reservoir	—	—	0.00	—
Marsh Unit 1, Columbia National Wildlife Refuge	—	—	0.00	—
Solstice Island, Potholes Reservoir	0.43	—	—	—
Three Mile Canyon Island, John Day Reservoir	0.00	—	—	—
Miller Rocks, The Dalles Reservoir	0.3	—	—	—
Badger Island, McNary Reservoir	0.00	—	—	—
Goose Island, Banks Lake	0.15	—	—	—
Regional average	0.39	0.29	0.33	0.34

* Breeding colonies where management occurred.

Crescent islands (Table 1). The colony at the Blalock Islands continued to be the largest in the region; however, colony size declined from 677 breeding pairs in 2015 to 483 breeding pairs in 2016. The small colony at Lenore Lake continued to grow in 2016, reaching 39 breeding pairs. Average nesting success at Lenore Lake in 2016 also increased to 0.59 fledglings/breeding pair (Table 2). Terns also formed a colony of 144 breeding pairs on a small sandy island in northeastern Potholes Reservoir (Table 1). The island used by terns in 2016 had not previously been used by breeding terns, and this nesting attempt failed to fledge any young before the colony was abandoned in early June.

Regional Population Size and Nesting Success

The number of Caspian terns breeding in the Columbia Plateau region during the premanagement period (2000–2013) was $\bar{x} = 877$ pairs (SD = 111.2, $n = 14$). There was no significant trend in the number of breeding pairs as a function of year during the premanagement period (2000–2013; $R^2 < 0.01$, $P = 0.94$). The estimated total number of breeding pairs in the Columbia Plateau region in 2015 was 769 pairs, significantly less than the premanagement average ($t_0 = -3.67$, $P \leq 0.005$). The estimated total number of breeding pairs in the Columbia Plateau region in 2016 was 675 pairs, also significantly less than the premanagement average ($t_0 = -6.84$, $P \leq 0.001$). "However, in neither 2015 nor in 2016 did the size of the Columbia Plateau subpopulation of Caspian terns come close to achieving the management goal of ≤200 breeding pairs (USACE 2014)."

The average annual nesting success for Caspian terns breeding in the Columbia Plateau region during the premanagement period was 0.39 (SD = 0.18, $n = 14$) fledglings raised/breeding pair. There was a significant downward trend in the average number of fledglings per pair as a function of year across the premanagement period (2000–2013; $R^2 = 0.43$, $P = 0.01$). Estimated average nesting success for Caspian terns in the Columbia Plateau region during 2015 and 2016 was 0.33 and 0.34 fledglings/breeding pair, respectively. Neither were significantly different from average annual nesting success during the premanagement period (2015: $t_0 = -1.45$, $P = 0.08$; 2016: $t_0 = -1.21$, $P = 0.12$).

There were a variety of factors that limited nesting success at tern colonies in the Columbia Plateau region. Factors that appeared to limit colony size included flooding due to fluctuating reservoir levels at the Blalock Islands, and possible interspecific competition on islands where terns were nesting immediately adjacent to larger gull colonies, such as Harper Island, Twinning Island, and Lenore Lake (Table 3). Disturbance and predation pressure by avian and terrestrial predators may have been related to tern colony failures at some sites, including Twinning Island and Harper Island. Predation on Caspian tern adults and chicks by an American mink (*Mustela vison*) was responsible for the failure of the breeding colony in northeastern Potholes Reservoir in 2016 (Table 3). Finally, low availability of forage-fish could have been responsible for poor nesting success at colonies located on smaller water bodies at greater distances from the Columbia River, including Harper Island and Lenore Lake (Table 3).

Dispersal

A total of 184 banded Caspian terns were classified as Breeders at either Goose Island in 2013 or Crescent Island in 2014. Of these Breeders, >80% returned to the region in 2015 and 2016. These birds experienced significantly different proportions of transitions from Plateau Breeder to other classifications following management than before management (2014–2015 transition: $P \leq 0.001$; 2015–2016 transition: $P \leq 0.001$; Fig. 2). The proportion of terns that remained Plateau Breeders between years declined from 0.910 during premanagement transitions to 0.609 during the 2014–2015 transition year ($P \leq 0.001$) and to 0.602 during the 2015–2016 transition year ($P \leq 0.001$; Fig. 2). The proportion of terns that transitioned from Plateau Breeder to Plateau Nonbreeder increased from 0.042 during premanagement transitions to 0.205 during the 2014–2015 transition year ($P \leq 0.001$) and to 0.243 during the 2015–2016 transition year ($P \leq 0.001$; Fig. 2). The proportion of terns that transitioned from Plateau Breeder to Unknown increased from 0.014 during premanagement years to 0.124 for the 2014–2015 transition year ($P \leq 0.001$) and to 0.155 for the 2015–2016 transition year ($P \leq 0.001$; Fig. 2). Finally, the proportions of terns that transitioned from Plateau Breeder to either Off-Plateau Breeder (2014–2015: $P = 0.999$; 2015–2016: $P = 0.176$) or to Off-Plateau Nonbreeder (2014–2015: $P = 0.043$; 2015–2016: $P = 0.999$) were not significantly different between the premanagement transition years and either transition year during management (Fig. 2). Thus, despite fewer terns remaining as Plateau Breeders during management, the

Table 3. Factors limiting colony size and nesting success at active Caspian tern colonies in the Columbia Plateau region, Oregon and Washington, USA (2015–2016).

Location	Factors limiting colony size and nesting success
Blalock Islands, John Day Reservoir	Flooded nests due to fluctuating reservoir levels
Twinning Island, Banks Lake	Possible predation pressure from terrestrial predators (mink) and avian predators (owls and diurnal raptors)
Harper Island, Sprague Lake	Pressure from neighboring gull colony; predation pressure from diurnal avian predators; possible lack of forage fish and food limitation
Lenore Lake	Possible lack of forage fish; interspecific competition for nest sites from gulls
Northeastern Potholes Reservoir	Predation by American mink
Finley Islands, McNary Reservoir	Flooding due to fluctuating reservoir levels
Marsh Unit 1, Columbia NWR	Possible predation pressure

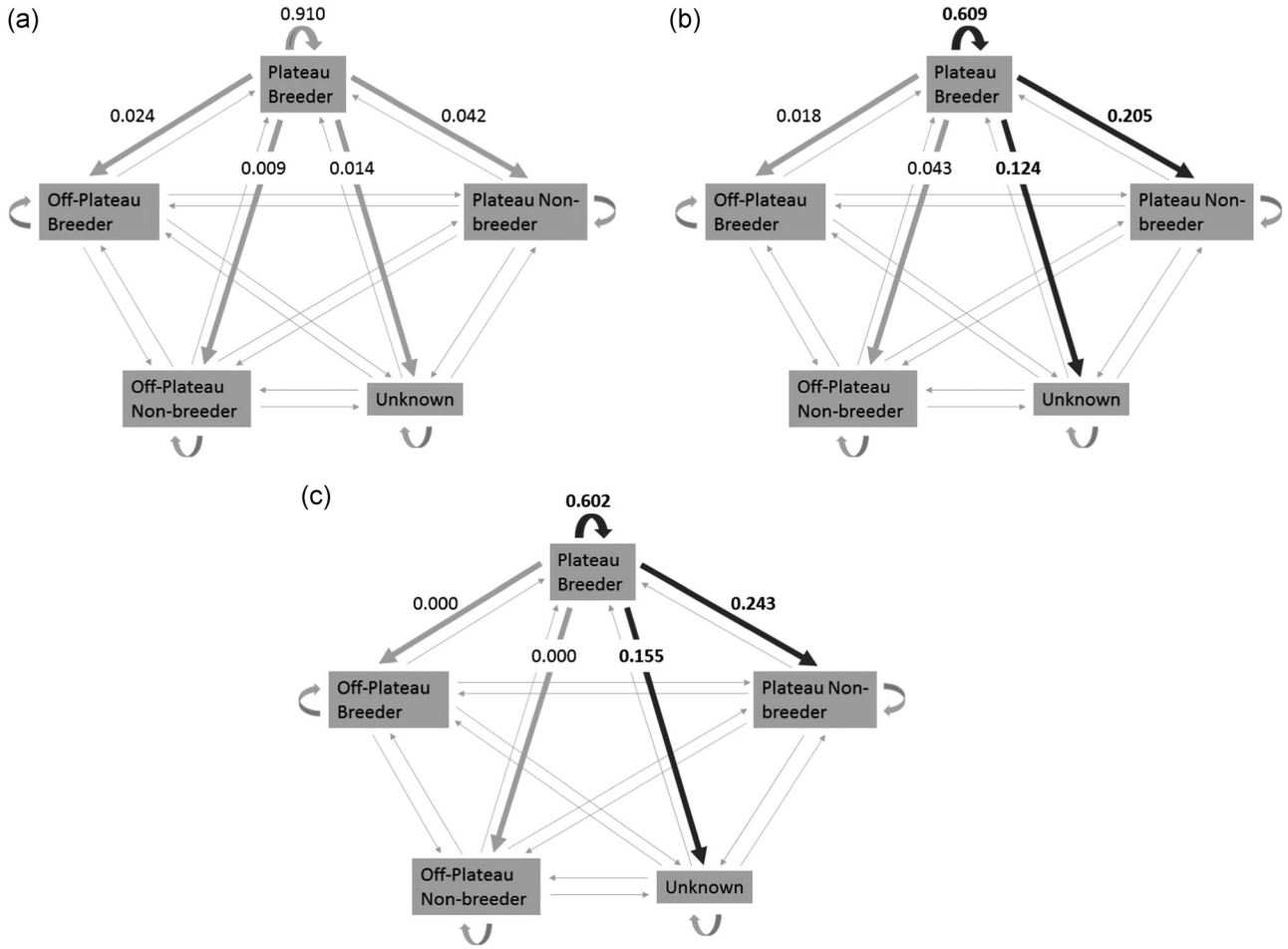

Figure 2. Proportions of all possible transitions of individually marked Caspian terns classified as Plateau Breeders to all possible statuses premanagement (a: 2011–2013) and years during management (b: 2014–2015 and c: 2015–2016) of breeding colonies in the Columbia Plateau region of Oregon and Washington, USA. Transition proportions during management that were significantly different from premanagement transition proportions are shown in bold ($P \leq 0.01$, the Bonferroni-adjusted significance threshold).

available band resighting data did not support the prediction that more terns would emigrate to other regions and breed or prospect for breeding opportunities there.

The proportion of transitions from Plateau Nonbreeder to other classifications did not differ between premanagement and 2014–2015 transitions ($P = 0.728$), but differed significantly in 2015–2016 ($P = 0.027$; Fig. 3). The proportion of terns that remained Plateau Nonbreeders in consecutive years increased from 0.081 during premanagement to 0.351 for the 2015–2016 transition year ($P = 0.009$). Transition proportions from Plateau Nonbreeder to all other breeding states during management remained similar to the premanagement period (Fig. 3).

DISCUSSION

Despite the demonstrated capacity of Caspian terns for long-distance breeding dispersal and quick establishment of new breeding colonies (Roby et al. 2002, Suzuki 2012), the number of nesting pairs in the Columbia Plateau region remained far higher in the first 3 years following implementation of management under the IAPMP than the plan's goal of ≤200 breeding pairs. Following the full implementation of the IAPMP, Caspian terns tended to shift to sites where small colonies were previously active or attempted to establish new colonies where nesting had not been previously observed (Lenore Lake).

Contrary to our prediction, analysis of resightings of banded terns failed to support increased emigration rates. These results were likely a reflection of the concurrent management to reduce available nesting habitat at East Sand Island in the Columbia River estuary, the largest Caspian tern breeding colony in the Pacific Flyway. In addition, drought conditions had a substantial impact on alternative colony locations throughout the southern Oregon and northeastern California (SONEC) region (Roby et al. 2015, 2016). These additional pressures on tern nesting habitat outside of the Columbia Plateau region may have rendered these locations unattractive to terns that previously nested at Goose Island or Crescent Island, and compelled terns to remain within the Columbia Plateau region and compete for nesting space at smaller active colonies or newly colonized nesting habitat. Analyses of resightings of Caspian terns banded as adults in the SONEC region revealed a large increase in net movement rates away

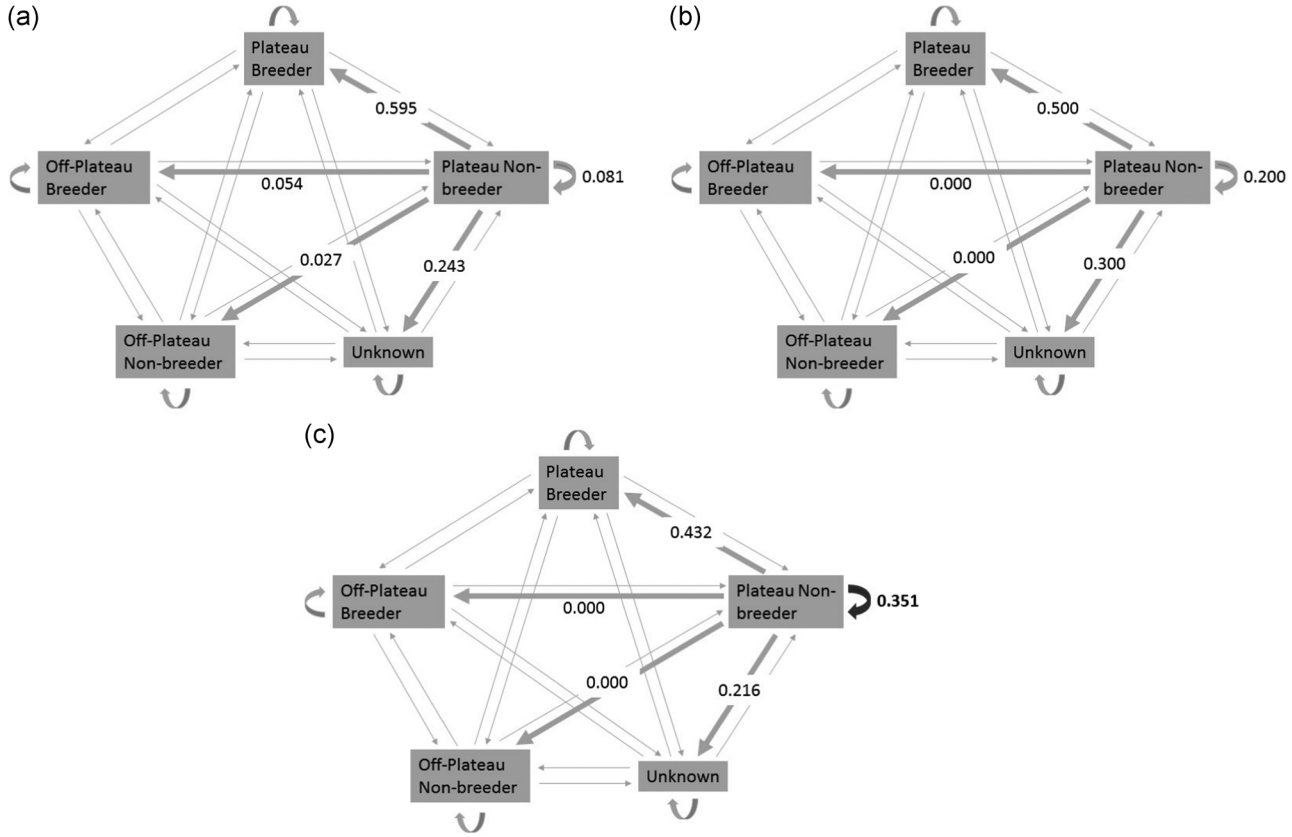

Figure 3. Proportions of all possible transitions of individually marked Caspian terns classified as Plateau Non-breeders to all possible statuses premanagement (a: 2011–2013) and years during management (b: 2014–2015 and c: 2015–2016) of breeding colonies in the Columbia Plateau region of Oregon and Washington, USA. Transition proportions during management that were significantly different from premanagement transition proportions are shown in bold ($P \leq 0.01$, the Bonferroni-adjusted significance threshold).

from colonies in the SONEC region to colonies in other regions of the Pacific Flyway, including the Columbia Plateau region, during 2014–2016, coincident with implementation of the IAPMP (Y. Suzuki, unpublished data).

Observations by the U.S. Geological Survey at newly constructed alternative nesting islands at Don Edwards National Wildlife Refuge (DENWR) in San Francisco Bay that were created as part of the IAPMP found that they were successful at attracting nesting pairs of Caspian terns beginning in 2015 (Hartman et al. 2018). Of the 52 banded Caspian terns observed at the newly constructed tern islands in DENWR during 2015–2017 (Hartman et al. 2018), only two were originally banded in the Columbia Plateau; neither of these banded individuals were part of the banded bird analysis in this study. Seventy-four percent of the 52 banded Caspian terns seen in DENWR during 2015–2017 were banded in San Francisco Bay, suggesting that the terns nesting on those newly constructed tern islands were mostly from the local region (Hartman et al. 2018).

Caspian terns have historically attempted to nest at 11 sites in the Columbia Plateau region, including Goose and Crescent islands. Staav (1979) and Cuthbert (1988) described Caspian tern nesting systems that consisted of a network of islands, some of which terns were able to utilize for nesting during periods when other sites within the system were unsuitable or unavailable. These studies did not describe extensive losses of nesting habitat formerly used by the majority of nesting terns in their respective study areas, but they highlight the flexibility of Caspian terns for changing nesting locations quickly in response to changes in availability of nesting habitat. Familiarity with potential alternative nesting habitat and other smaller active colonies within the region could facilitate the establishment of new or larger colonies locally, and lead to minimal emigration outside the region in search of prospective breeding sites (McNicholl 1975).

Prior knowledge of good alternative nesting habitat may inform displaced terns where they can potentially breed successfully. The Blalock Islands and Crescent Island are both located on the Columbia River; therefore, it is very likely that Caspian terns that nested at Crescent Island encountered the Blalock Islands during foraging trips or migration prior to the onset of management. Familiarity with the Blalock Islands is especially likely given that terns have actively nested within this archipelago in small numbers since 2005 and the straight line distance between Crescent Island and the Blalock Islands is about 60 km, well within the distance at which terns nesting in the Columbia Plateau region have been documented foraging from their nest site (max. 93 km, D. E. Lyons et al., unpublished data). Additionally, in the 2 years prior to the implementation of the IAPMP, 2012 and 2013, the Blalock Islands were the

site of the only active Caspian tern colony other than Goose Island and Crescent Island where young were successfully fledged. As the next most productive breeding location immediately prior to the initiation of management, prior knowledge of the Blalock Islands colony may have informed terns that this site could be productive nesting habitat in a region already familiar to them (Danchin et al. 1998, Naves et al. 2006). Smaller, previously active tern colonies that remained small and failed to produce young during management did so probably because of the presence of predators that present a potential threat to adult survival (Conover and Miller 1979).

After the full implementation of the IAPMP, regional reproductive success did not decline significantly compared with the premanagement average. In addition, nesting success in 2015 and 2016 stayed at the low end of the range considered sufficient to maintain a stable population (0.32–0.74 young fledged/breeding pair; after Suryan et al. 2004). The reasonably high nesting success following full implementation of management could have further incentivized terns to stay and compete for nesting space on the Columbia Plateau, especially if environmental conditions remained unfavorable at other potential colony locations outside of the Columbia Plateau region.

Terns that remain in the Columbia Plateau region as nonbreeders could at least temporarily offset some of the potential management benefits for survival of salmonid smolts by continuing to forage in the region during a sabbatical from nesting. As nonbreeders, these adults could still target juvenile salmonids during the out-migration because they are not bound by central-place foraging around a particular nesting site. Data on the movements of satellite-tagged terns during 2014–2016, the first 3 years of management under the IAPMP, found that the elimination of the tern colonies at Goose and Crescent islands only resulted in limited dispersal of terns away from the Columbia Plateau region (D. E. Lyons et al., unpublished data), consistent with the analysis of banded tern movements presented here. Measures of predation on juvenile salmonids by terns from Potholes Reservoir were reduced, but this benefit was offset by increased predation by terns nesting at the Blalock Islands (Roby et al. 2015, 2016).

Most terns displaced by the elimination of the Goose and Crescent island colonies remained in the Columbia Plateau region, at least for the first 2 years following full implementation of the IAPMP. Remaining a nonbreeder while competing for nesting space in familiar habitat is a strategy that may improve an individual's reproductive value by enhancing the prospects for breeding in quality habitat (Zack and Stutchbury 1992, Naves et al. 2006). This potential strategy was supported by the increase in the proportion of nonbreeders in the Plateau region, and little to no corresponding increase in the proportion of emigrants from the Plateau region. Terns employing this strategy could enhance their fitness by remaining nonbreeders while competing for nesting space at active colonies, replacing failed breeders, or establishing new colonies. It seems unlikely, however, that terns that became nonbreeding floaters in the Columbia Plateau region as a result of the implementation of the IAPMP would remain so indefinitely.

Despite the flexibility exhibited by terns for nest site selection after full implementation of the IAPMP, results of analysis suggest that current and potential colony locations in the region do not provide sufficient nesting space to maintain historical numbers of nesting pairs. We expect that in the future a higher proportion of terns will emigrate from the Columbia Plateau region if they are unable to raise young successfully in the region. Naves et al. (2006) suggested that long-lived seabirds might integrate information from several consecutive breeding failures before making a decision to immigrate to a new region to breed. Adult Caspian terns with a history of regular nesting in the Columbia Plateau region that have not yet emigrated still might do so in larger numbers, especially if environmental conditions improve at potential nesting locations outside the Columbia Plateau region. For example, if drought conditions ease in the SONEC region, terns that have expended energy competing for nesting space in marginal habitat in the Plateau region during the early years of management might be more motivated to emigrate to these alternative colony locations.

In response to the loss of the majority of quality nesting habitat available within the region due to management, most terns were able to take advantage of other active, former, or prospective nesting habitat within the Columbia Plateau region that is potentially less conducive to nesting success than the former colony sites on Crescent and Goose islands. Some of the potential benefits to survival of salmonid smolts from the implementation of the IAPMP may have been offset in the short term by an increase in the numbers of nonbreeding terns that continue to consume juvenile salmonids in the region, but whose movements and foraging behavior are difficult to monitor. The marginal nature of nesting habitat chosen by terns after the implementation of the IAPMP may eventually act to more severely restrict the numbers of nesting pairs within the Columbia Plateau region. If environmental conditions remain similar in the future, we would expect that the number of Caspian tern nesting pairs in the Columbia Plateau region will continue to gradually decline as existing colony locations experience partial breeding failures (e.g., the Blalock Islands) or complete breeding failures (e.g., northeastern Potholes Reservoir). Indeed, the analysis of resightings of banded terns suggests that terns may be slowly emigrating from the Columbia Plateau region. If conditions remain unfavorable at alternative colony sites outside of the Columbia Plateau region, however, the majority of terns may continue to prospect and compete for limited nesting space within the region.

MANAGEMENT IMPLICATIONS

The 2-year duration of this study may not be sufficient to accurately assess the long-term response of Caspian terns to the IAPMP. In the short term, Caspian terns may stay and compete for an opportunity to breed, especially if poor conditions for breeding exist elsewhere and there is a history

of nesting at multiple locations in the region. Terns may integrate information on several failed breeding attempts or changes in environmental conditions outside of the Columbia Plateau region before emigrating in larger numbers, and thus eventually meeting the management objective for size of the regional subpopulation. Management of long-lived seabirds requires planning for short-term responses before long-term objectives are met. Additionally, managers seeking to use nonlethal nesting habitat management to reduce conflicts between piscivorous birds and fish of conservation concern should develop appropriate expectations for required project durations. This is especially the case when alternative nesting habitat is marginal, distant, or only intermittently available, and there is a history of nesting at multiple locations within the region, sites that terns could potentially utilize in the short term.

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