short communication *Wader Study* 124(2): 00–00. doi:10.18194/ws.00071

Lessons learned from the oldest Snowy Plover

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Keywords: *Charadrius nivosus*, dispersal, longevity, reproductive success, Snowy Plover, threatened

Ornithologists and conservationists are well aware of the valuable insights provided by long-term studies of populations of individually marked animals (Clutton-Brock 1988, Newton 1998). In particular, estimates of survivorship and reproductive success derived from annual records of uniquely marked birds inform management practices that attempt to increase population size, which is especially important for threatened and endangered taxa (e.g., Pakanen 2016). Recently, we summarized population growth (Colwell *et al.* 2017), lifetime reproductive success (Herman & Colwell 2015), and annual variation in survivorship (Mullin *et al.* 2010, Colwell *et al.* 2013) for the Snowy Plover *Charadrius nivosus*. Here, we submit observations of a male Snowy Plover (Fig. 1) who, at 16 years of age, continues to offer insight into the conservation challenges faced by the species.

Fig. 1. OR:YR, the oldest Snowy Plover on record, hatched on 26 June 2001; on 26 June 2017 he hatched three chicks at Big Lagoon.

Longevity – On 26 June 2001, we banded a newly hatched Snowy Plover at Eel River Wildlife Area in Humboldt County, California, USA (Fig. 2). One year later (3 August 2002), we recaptured him as a breeding adult at Clam Beach and uniquely marked him OR:YR. In 2017, this 16-year-old male continued to breed and winter locally; observers detected him most recently in July 2017. His age represents a longevity record for the species (L.E. Stenzel & D.J. Lauten pers. comm.) and, quite possibly, for the 34 species of *Charadrius* worldwide (Dinsmore in press). For the clade, however, multiple Wrybills *Anarhynchus frontalis* far surpass this longevity record, with two birds reaching 22 years (A.C. Riegen pers. comm.).

Dispersal – The distance (~38 km) between OR:YR's natal nest and his first breeding attempt was comparable to other philopatric plovers in our population (Colwell *et al.* 2007, Pearson & Colwell 2013), with the largest percentage of males (38%) and females (54%) first breeding 10–100 km from their natal site. In his first seven years (2002–2008), OR:YR bred and wintered exclusively on Clam Beach, a site characterized by high activity of Common Ravens *Corvus corax*, an important egg predator in our study area (Burrell & Colwell 2012). To increase nest survival, we routinely protected clutches with predator exclosures erected around nests (i.e., 122 nests over 2002–2006; Hardy & Colwell 2008). In 2009, OR:YR first bred on Clam Beach before he and his mate disappeared; observers later found him ~45 km north at Stone Lagoon, tending 10-day-old chicks. In the subsequent years (2010–2016) he increasingly bred at Stone Lagoon. In winter, we regularly observed OR:YR on Clam Beach, although he occasionally occupied other sites (Big Lagoon; Nov 2016–Jul 2017). In our study population, males typically disperse shorter distances than females. Furthermore, males tend to be more site-faithful after successfully hatching chicks (median: 0.7 km; range: 0.2–1.4) compared with failed nests (median: 1.3 km; range: 0.4–3.0); similar patterns obtain in comparisons of movements between years (Pearson & Colwell 2013).

Reproductive success – Dispersal is often associated with reproductive success (Oring & Lank 1984). Along the Pacific coast, Snowy Plovers initiate nests from early March until late July, with multiple opportunities to replace failed clutches (Warriner *et al.* 1986). During his first five years, we protected 11 of OR:YR's 17 nests using exclosures. As a 2-year-old, he successfully hatched four chicks from his first two exclosed nests; none of these chicks fledged. Additionally, seven (64%) of his exclosed nests failed to hatch eggs and only one produced fledglings. In 2006, we stopped using exclosures because six to eight incubating adults (~20% of breeding adults at the site)

disappeared. We presumed that an unknown vertebrate predator had consumed these individuals as evidenced by at least one deceased adult and the absence of others when they should have been incubating (Hardy & Colwell 2008, Mullin *et al.* 2010). We did not protect his subsequent nests on Clam Beach. In 2007, OR:YR initiated 10 nests with a female (WW:YG) who laid 22 eggs over the breeding season; they did not hatch offspring that year. OR:YR's attachment to Clam Beach may have stemmed from his early success at hatching eggs in nests that we protected with exclosures; however, mate fidelity also may have played a role (Pearson & Colwell 2013). Over his 15-yr breeding history, OR:YR averaged 1.7 (range: 1–4) mates annually; in 47% of years, he bred with a single female for the entire breeding season.

Lifetime reproductive success of plovers has a strong pattern of unequal progeny production (Koenig 1988). In a sample of 195 Snowy Plovers, 13% of individuals (12 males; 14 females) produced 50% of fledged young (Herman & Colwell 2015). Over his lifetime, OR:YR tended 148 eggs in 58 nests, and hatched 31 chicks, of which 13 fledged (i.e., reached 28 days of age). His fledging success makes him the second most prolific breeder in our population, in which males averaged 2.2 ± 3.0 fledged young over their lifetimes (Herman & Colwell 2015). However, given his age, OR:YR was well below the reproductive output expected for an individual who has bred for 16 years. Most (9 of 13) of his fledglings originated from Stone Lagoon in the second half of his life. We estimated breeding efficiency as the ratio of chicks fledged to eggs tended; briefly, a perfectly efficient breeder produces a fledged chick for every egg tended (1.0) compared with one that never produces offspring (0.0). At Clam Beach, OR:YR produced 0.03 fledglings per egg, whereas at Stone Lagoon he was ten times more efficient (0.30 fledglings per egg).

Conservation implications – The longevity, dispersal and reproductive success exhibited by OR:YR highlight the impacts of commonly used management practices aimed at recovering the population size of this threatened taxon (USFWS 2007). For example, we used non-lethal predator management (i.e., nest exclosures) to increase reproductive success at the site where OR:YR bred early in his life. We suspect that his success as a young breeder affected his decision to be site-faithful to Clam Beach (Oring & Lank 1984). Furthermore, differences in reproductive success between sites correlate with activity of predators. For example, nest predation rate correlates positively with Common Raven presence and abundance across our study area (Burrell & Colwell 2012). Clam Beach ranks among sites with highest raven activity (1.43 ± 0.51 ravens detected on 40% of point counts averaged across 10 years) compared with Stone Lagoon (0.56 ± 1.54 ravens detected on 17% of point counts). Increased management to reduce the negative impacts of predators on plover reproductive success is warranted. Finally, the population of Snowy Plovers in coastal northern California is small (19–74 breeding adults annually; Colwell *et al.* 2017), though connected by dispersal to populations elsewhere along the Pacific coast (Stenzel *et al.* 1994, Colwell *et al.* 2007, 2017, Pearson & Colwell 2013). Consequently, the effective population size is likely equivalent to the entire listed population segment (i.e., ~2200 adults in 2016; *https://www.fws.gov/Arcata/es/birds/WSP/plover.html*). We occasionally observe instances of inbreeding locally (Colwell & Pearson 2011), and the genes of individuals that live as long as OR:YR may be disproportionately represented in the population. If so, this may require additional study regarding the role of inbreeding in isolated populations of the Snowy Plover.

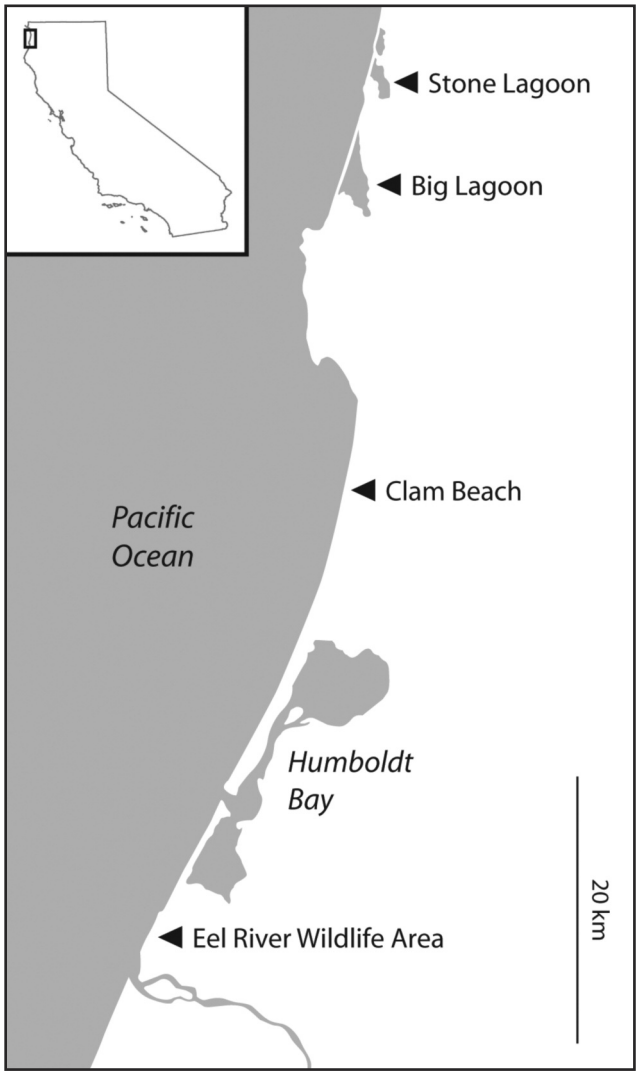

Fig. 2. Study area in coastal northern California, USA. OR:YR hatched at Eel River Wildlife Area and bred at Clam Beach, Stone Lagoon, and Big Lagoon.

We thank the many field assistants who have worked on this project over the past 17 years. Support for our research came from the California Department of Fish and Wildlife, California Department of Parks and Recreation, U.S. Bureau of Land Management, U.S. Fish and Wildlife Service, and California Department of Fish and Game's Oil Spill Response Trust Fund through the Oiled Wildlife Care Network at the Wildlife Health Center, School of Veterinary Medicine, University of California, Davis.

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