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Breeding efficiency: a metric for assessing habitat quality and individual performance?

Mark A. Colwell*, Katelyn M. Raby & Elizabeth J. Feucht

Wildlife Department, Humboldt State University, Arcata, CA 95521, USA
Corresponding author: mac3@humboldt.edu

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Assessment of habitat quality and individual reproductive performance are vital facets of conservation, which often prompt management actions to increase population size. Here, we present a metric (breeding efficiency; BE) for gauging productivity (of sites or individuals), which uses the ratio of chicks fledged to eggs laid; BE can be further dissected into egg efficiency (EE; hatchlings:eggs) and chick efficiency (CE; fledglings:hatchlings). Our data come from intensive, long-term (i.e., 18 yr) monitoring of a marked population of the Pacific coast Snowy Plover *Charadrius nivosus*, which is listed as threatened under the U.S. Endangered Species Act. Overall, BE averaged 0.19 ± 0.25 across sites and years (n = 126). BE correlated negatively with the number of nests (–0.13, P = 0.07), which likely stemmed from frequent renesting following clutch failure at some sites. BE also differed among sites, which suggests that habitat quality varied with predation, the principal cause of reproductive failure in the population. A strong positive correlation (0.92) between BE and per capita fledging success (across sites and years; n = 106, excluding sites with predator exclosures at nests) suggests that BE can be applied to populations that are unmarked and less intensively monitored. The latter case may be accomplished by locating nests or incubating adults (assuming a completed clutch) and tallying fledged chicks at intervals of several weeks.

Keywords

breeding efficiency

Charadrius nivosus

habitat quality

monitoring

per capita fledging success

population growth

Snowy Plover

threatened

INTRODUCTION

Loss and degradation of habitat is the single most important factor driving the contemporary biodiversity crisis (Brooks *et al.* 2002). Consequently, quantifying and monitoring habitat quality is a foundation of conservation because it prompts management decisions aimed at ameliorating population declines (Colwell 2010). Moreover, adaptive management requires information to evaluate the outcome of conservation practices. Habitat quality may be quantified directly by measuring physical features of the environment such as vegetation structure and composition, food availability, predator abundance or disturbance by humans, all of which influence individual fitness via effects on vital rates (Morrison *et al.* 2012). For example, the suitability of habitat for breeding shorebirds is often gauged based on measures of vegetation density. For species that conceal their nests, this may be related to predation risk to eggs, which influences reproductive success (e.g. Koivula & Rönkä 1998). By contrast, plovers favor open, sparsely vegetated areas that afford an unobstructed view to detect approaching predators (Colwell 2010). Alternatively, indirect measures derived from the breeding performance of individuals can be used to gauge habitat quality (Morrison *et al.* 2012). While the number of nests in an area may be informative about habitat quality, frequent renesting following clutch failure could produce a misleading indicator of habitat quality (sensu Van Horne 1983) if few nests produced chicks or fledglings. Ideally, high quality habitat is that which supports vital rates (i.e., productivity, adult survival) that result in positive population growth. For example, Snowy Plovers *Charadrius nivosus* experienced high annual and lifetime reproductive success when breeding on riverine gravel bars where heterogeneous substrates afforded crypsis to eggs and chicks (Colwell *et al.* 2011, Herman & Colwell 2015).

In a recent paper (Colwell *et al.* 2017b), we introduced breeding efficiency (BE) as a simple metric to gauge the reproductive performance of individuals. We estimated BE as the ratio of number of fledged chicks to eggs laid

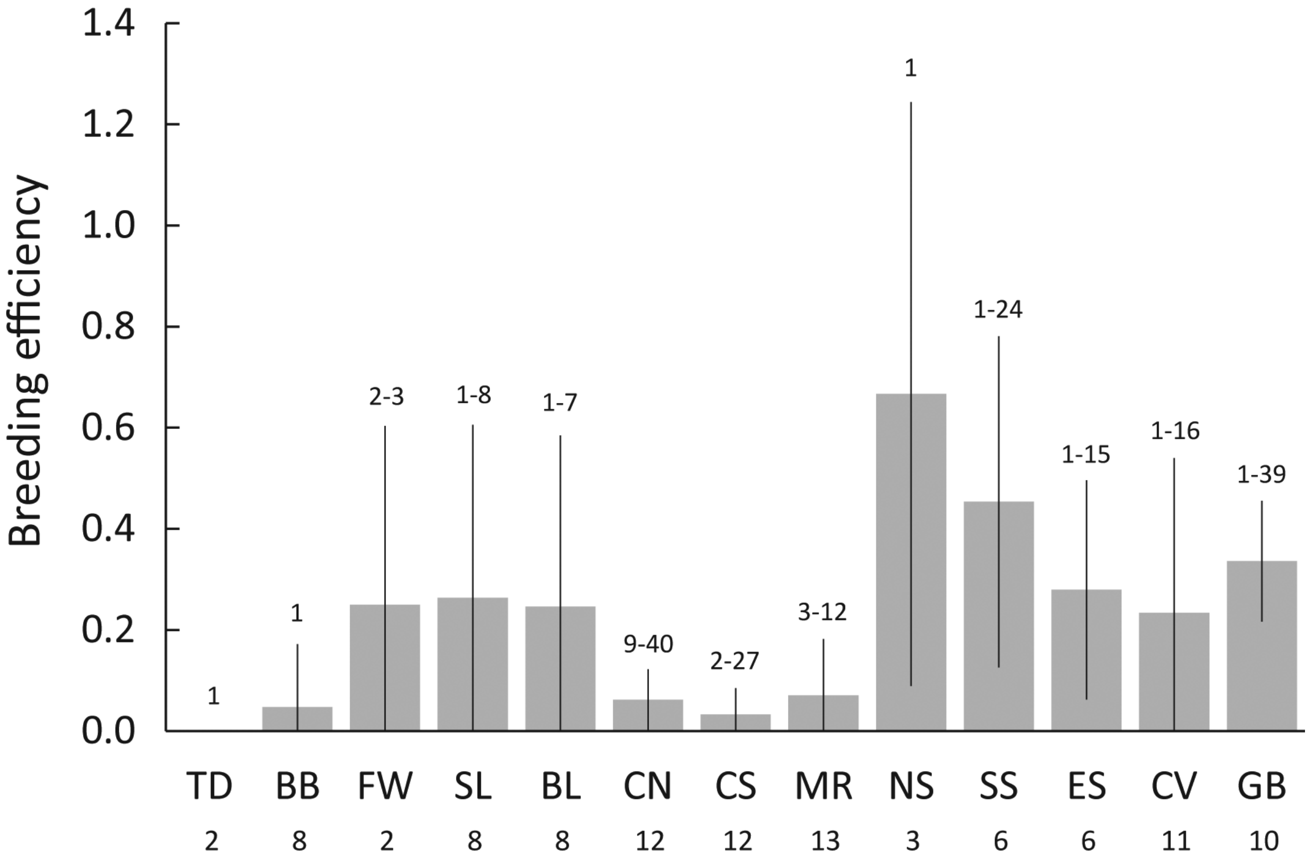

Fig. 1. Snowy Plover breeding efficiency (mean, SD) varied greatly across 13 sites at which plovers bred in Humboldt County, California. Numbers above histogram show the range of number of nests across years in which plovers bred, which is shown below the horizontal axis legend. From north (left) to south (right), the sites are TD = Tolowa Dunes, BB = Gold Bluffs, FW = Freshwater Lagoon, SL = Stone Lagoon, BL = Big Lagoon, CN = North Clam Beach, CS = South Clam Beach, MR = Mad River Beach, NS = North Spit, SS = South Spit, ES = Eel R. Wildlife Area, CV = Centerville, and GB = multiple gravel bars along the lower Eel River.

(or tended) by an individual or population. As such, BE varies between 0.0 and 1.0, corresponding to situations in which no and all chicks fledge, respectively, from the number of eggs laid. Here, we further develop this metric using 18 years of data from an intensively monitored population of individually marked Snowy Plovers (Colwell *et al.* 2017a), and apply it to habitats and populations.

METHODS

Study area

We have monitored a color-marked population of Snowy Plovers since 2001 in coastal northern California (see Colwell *et al.* 2017a), which constitutes one of six recovery units designated in the species' recovery plan (USFWS 2007). Our most intensive monitoring has occurred along ~100 km of ocean-fronting beaches (80 km) and riverine gravel bars (15 km) in Humboldt County, where plovers have bred in loose aggregations (as gauged by distance to nearest conspecific nest) that vary inversely with population size (Patrick & Colwell 2018). The quality of breeding habitat, as gauged by individual reproductive success (i.e., per capita fledging success; PCFS) has varied annually and across habitats. In most years, average PCFS is below 1.0; although in the past three years (2016–2018) this value has increased dramatically (Feucht *et al.* 2018). Variation in PCFS appears to be most strongly associated with habitat features that offer greater crypsis to eggs (Colwell *et al.* 2011) and chicks (Herman & Colwell 2015). Elsewhere, we present a detailed description of the study area (e.g., Colwell *et al.* 2017a and references therein). We organized our results by 'site,' which corresponds to the government (county, state, or federal) entity responsible for management (Fig. 1).

Field methods

Each year, observers surveyed for breeding plovers beginning in mid-March, when plovers laid their first eggs, and continued until the last chicks fledged in late August or September. During surveys, observers walked linear stretches of beach or gravel bar, stopping frequently to scan for plovers with binoculars and a spotting scope. On ocean-fronting beaches, we often used tracks in the sand to help find courtship scrapes and nests (Muir & Colwell 2010). At all sites, we collated observations of color-marked individuals, maintained nest records detailing

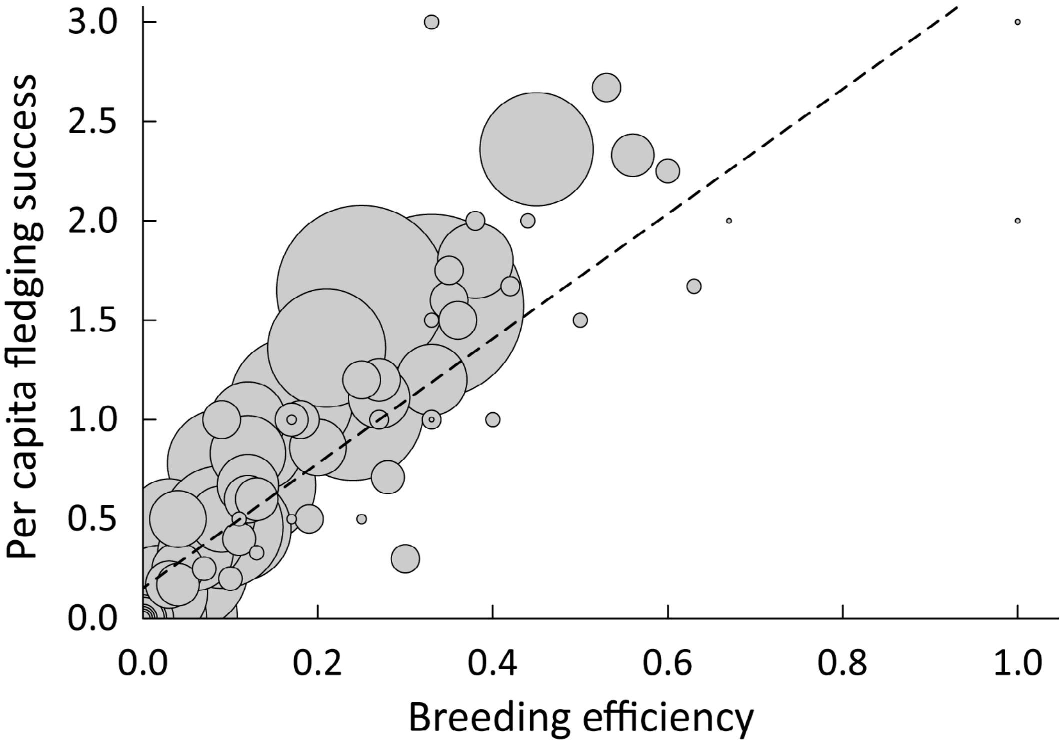

Fig. 2. Snowy plover per capita fledging success correlated positively with breeding efficiency across multiple years and breeding locations. Relative bubble size equals sample size (i.e., number of nests; see Table 1) for each site and year.

fates and timing of failure or hatch, and monitored the survival of chicks until they fledged at 28 d (Page *et al.* 2009). These data provide the basis for calculations of BE and its components. In most years, we surveyed sites at approximately weekly intervals, supplemented by observations from agency biologists and consultants. If observers detected plovers or evidence of breeding (i.e., courtship scrapes), we increased the frequency of surveys.

Over 18 years, size of the study population varied between 19–74 (Table 1), which has facilitated our banding of nearly all breeding adults (~95% annually) and newly hatched chicks (Colwell *et al.* 2017a). Accordingly, we maintain detailed records of individual breeding performance including annual and lifetime totals for number of: 1) eggs laid (females) or tended (males); 2) chicks hatched; and 3) juveniles fledged (see Colwell *et al.* 2013, Herman & Colwell 2015). From these data, we derived annual mean (±SD) PCFS for males breeding at each site, which is a criterion for delisting under the U.S. Endangered Species Act (USFWS 2007).

Data summary

Our approach to indexing habitat quality is based on the breeding activity of individually marked plovers (see Colwell *et al.* 2017b). To derive our metric, breeding efficiency (BE), we collated data based on the number of eggs tended, chicks hatched, and juveniles fledged for males breeding at different sites within the study area. We calculated BE as the total number of fledged juveniles divided by the total number of eggs. Similarly, egg efficiency (EE) was the total number of hatched chicks divided by total eggs; chick efficiency (CE) was the total number of fledged juveniles divided by the total number of chicks hatched. BE is the product of EE and CE.

RESULTS

Over 18 years (Table 1), we monitored 1,055 plover nests, in which females laid 2,625 eggs. In total, these nests hatched 900 chicks and fledged 484 juveniles. These data yielded a BE of 0.185, which is the product of EE (900/2625 = 0.343) and CE (484/900 = 0.538).

Overall, BE varied greatly among sites and years (Table 1; Fig. 1). At several adjacent sites (North and South Clam Beach, Mad River Beach) where plovers bred each year, BE was chronically low (0.06 ± 0.06, 0.03 ± 0.05 and 0.07 ± 0.11, respectively). By contrast, at several other locations (e.g., South Spit, Centerville Beach, and gravel bars), BE was significantly higher (0.46 ± 0.33, 0.23 ± 0.31, and 0.34 ± 0.12, respectively; $F_{5,51} = 8.19$, $P < 0.0001$).

BE and reproductive success

To explore the relationship between BE and PCFS, we collated data across 13 sites, at which we found 1–40 nests during 1–18 years of monitoring (Fig. 1). We were motivated in this analysis by the recovery objective (i.e., for delisting), which uses a benchmark of 1.0 fledged chick per male for five years (USFWS 2007). Overall, there was a strong positive correlation between BE and PCFS (Fig. 2) whether derived from annual means across

Table 1. Annual variation in breeding efficiency of Snowy Plovers as indexed by the ratio of young fledged to eggs laid.

	2001	2002	2003	2004	2005	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018
No. breeding plovers	58	63	55	74	66	59	30	36	19	32	36	39	44	51	61	72	72	63
Total nests	57	75	73	64	54	57	41	50	35	42	32	41	58	55	58	64	82	75
Total eggs laid	153	188	185	158	140	150	100	113	81	99	88	106	147	118	149	166	192	175
Total chicks hatched	97	76	64	66	70	52	21	15	15	24	35	39	32	27	48	65	74	80
Total young fledged	46	23	32	36	27	20	11	8	9	13	8	15	17	17	27	40	39	48
Tolowa Dunes (2)[a]	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.00	0.00	-
Gold Bluffs (7)	-	-	-	0.33	0.00	-	-	-	-	-	-	-	0.00	0.00	0.00	-	-	0.00
Freshwater Lagoon (5)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.50	0.00
Stone Lagoon (24)	-	-	-	-	-	-	-	-	1.00	0.50	0.00	-	-	0.40	0.33	0.09	0.00	0.00
Big Lagoon (24)	-	-	-	-	0.00	-	-	-	-	-	0.44	0.17	-	0.00	0.00	1.00	0.19	0.17
N. Clam Beach (336)	0.25	0.00	0.03	0.16	0.17	0.05	0.02	0.00	0.00	0.00	0.04	0.11	0.17	0.00	0.10	0.13	0.09	0.06
S. Clam Beach (214)	0.17	0.07	0.09	0.09	0.14	0.12	0.04	0.00	0.00	0.00	0.13	0.12	0.00	0.00	0.00	0.00	0.10	0.00
Mad River Beach (64)	-	-	-	-	-	0.00	0.10	0.00	0.00	0.00	0.00	0.00	0.00	0.04	0.18	0.27	0.30	0.18
North Spit (3)	-	-	-	-	-	-	-	-	-	-	-	-	-	0.00	-	1.00	-	1.00
South Spit (64)	-	-	0.00	0.00	0.33	0.40	1.00	0.33	-	0.00	-	-	-	-	-	0.56	0.43	0.45
Eel R. Wildlife Area (78)	0.29	0.03	0.00	0.00	-	-	0.00	0.26	0.33	0.07	0.00	0.63	0.35	0.25	0.33	0.11	0.33	0.67
Centerville (63)	-	-	-	1.00	-	0.00	-	-	-	0.00	0.11	0.00	0.00	0.53	0.32	0.20	0.13	0.33
Gravel bars (171)	0.33	0.24	0.25	0.21	0.27	0.27	0.45	0.44	0.33	0.60	-	-	-	-	-	-	-	-
Total[b]	0.30	0.12	0.17	0.23	0.19	0.13	0.11	0.07	0.11	0.13	0.09	0.14	0.12	0.14	0.18	0.24	0.20	0.28

[a] Total number of nests; [b] Total fledged young/total eggs laid.

sites (r = 0.92, P < 0.0001, n = 13) or based on individual site-years (r = 0.92, P < 0.0001, n = 126). At several sites, we used nest exclosures in multiple (n = 20 site*years) to improve hatching success. When we omitted these observations, the relationship between BE and PCFS remained unchanged (r = 0.92). Importantly, 93% of sites with a BE ≥ 0.20 had a PCFS value ≥ 1.0. EE and CE correlated positively (r = 0.41, P < 0.0001, n = 105), indicating that sites that hatched a low percentage of chicks from eggs also fledged a small percentage of chicks from those that hatched. Finally, BE correlated negatively (–0.13, P = 0.07) with number of nests across sites.

DISCUSSION

Our results, derived from an intensively monitored population of individually marked plovers (Colwell *et al.* 2017a), provide several important insights into habitat quality with consequences for plover management and conservation. First, BE provides an index of habitat quality derived from the breeding performance of individuals occupying an area; we suggest that BE better represents habitat quality than the number of breeding adults in an area or number of nests. Second, BE may be an acceptable surrogate for PCFS, which means that simple counts of nests (assuming 3 egg clutches for plovers) and fledged chicks may suffice for less intensively monitored populations, especially those with a large percentage of unmarked individuals.

Habitat quality

Shorebird biologists have indirectly measured the quality of breeding habitat in a variety of ways, including breeding (or nesting) density (e.g., Brown *et al.* 2007), clutch or chick survival (e.g., Dinsmore *et al.* 2014, 2017), or individual reproductive success (e.g., Herman & Colwell 2015). Each of these measures has its shortcomings or challenges. For example, nesting density may not accurately represent habitat quality (Van Horne 1983) if high rates of predation cause frequent clutch failure and re-nesting. In this case, high nest density results from low clutch survival. For Snowy Plovers, an inverse relationship between BE and number of nests across sites and years supports this contention. However, the sites at which we monitored plovers vary in size, with plovers aggregating in loose associations in most years (Patrick & Colwell 2018). Additionally, we have not quantified nest density to directly assess the relationship between nest density and BE. Nevertheless, within our study area, the contrast between Clam Beach and Mad River Beach and several other sites (South Spit, Eel River gravel bars) is illustrative (Fig. 1). Clam Beach has chronically low BE, but always hosts breeding plovers that frequently re-nest; at least one pair re-nested 10 times (23 eggs) within a breeding season and failed to produce fledglings (Colwell *et al.* 2017b). By contrast, South Spit and the riverine gravel bars average higher BE. The cause of low BE at Clam Beach is egg predation by corvids (Common Raven *Corvus corax*, American Crow *C. brachyrhynchos*; Burrell & Colwell 2012), whereas egg and chick survival are higher where cryptic substrates afford camouflage for eggs and chicks (Colwell *et al.* 2011, Herman & Colwell 2015). Finally, the positive correlation (0.41) between EE and CE indicates that the use of exclosures to boost hatching success may not be effective in achieving increased PCFS because the loss of eggs is associated with similar rates of chick mortality; conversely, sites with high hatching success should produce high fledging success. This result has management implications. For example, it calls into question the exclusive use of exclosures as a non-lethal tool to boost plover productivity, especially given the cautions about elevated adult mortality (Hardy & Colwell 2008).

Monitoring

An obstacle for effective monitoring of the Snowy Plover is the logistical challenge associated with estimating PCFS as a requirement for delisting (USFWS 2007). Traditionally, biologists have marked adults and chicks, and monitored their survival to fledging age to derive this metric, but this is labor intensive and costly. We have been able to maintain a long-term database on annual and lifetime

Table 2. Examples of how application of breeding efficiency might be used to evaluate or monitor individual performance, habitat quality, and population response, with recent examples from *Charadrius* plovers.

Level of monitoring	Example	Reference
Individual	Age- or experience-related variation in reproductive success	Colwell *et al.* 2017b
	Predictor of breeding dispersal or mate change	Pearson & Colwell 2014
Habitat	Effectiveness of predator management on increasing productivity	Dinsmore *et al.* 2014, 2017
	Index of habitat quality following restoration	Lafferty *et al.* 2006 Catlin *et al.* 2015
	Consequence of varying human disturbance	Weston in press
Population	Surrogate for vital rate (e.g., PCFS)	This study
	Index of reproductive effort as a covariate with survival	Colwell *et al.* 2013

reproductive success (Herman & Colwell 2015) owing to the comparatively small population we studied (Colwell *et al.* 2017a). However, elsewhere in the species' range, where local populations number several hundred (Eberhart-Phillips *et al.* 2015), a challenge exists in marking a sufficient proportion of adults and following broods to derive an estimate of PCFS. We suggest that BE may be a reasonable surrogate for PCFS, as evidenced by the strong positive correlation between BE and PCFS, and the observation that nearly all sites with BE ≥ 0.20 produced a PCFS ≥ 1.0.

The recovery plan for the Western Snowy Plover (USFWS 2007) identified two recovery objectives necessary for delisting, one of which was maintaining PCFS ≥ 1.0 for five consecutive years within each of six recovery units. If we are correct that BE is a surrogate for PCFS, then a principal challenge of plover monitoring (best gauged using individually marked birds) may be attainable with unmarked populations. Furthermore, periodic (e.g., bimonthly, depending on breeding population size) surveys to document the number of nests in an area, accompanied by similarly timed counts to document fledged chicks of different age (see Bolton *et al.* 2011) may provide the critical data for PCFS. This notion, however, requires further testing.

We suggest that BE may have additional applications in conservation (Table 2). For instance, recently we used BE to summarize the reproductive history of a male in our study area who is the oldest Snowy Plover on record (Colwell *et al.* 2017b). This individual had two distinct episodes (early vs. late) in his life, during which BE increased ten-fold subsequent to his dispersal from Clam Beach to breed approximately 40 km north at Stone Lagoon and Big Lagoon. Early on, his decision (i.e., dispersal behavior) to remain at an unproductive site (i.e., low BE) may have been influenced by our use of exclosures to protect his eggs from predators (Hardy & Colwell 2008). In fact, we exclosed 11 of his first 17 nests (Colwell *et al.* 2017b). Given the relationship between hatching success and site fidelity (Pearson & Colwell 2014), we propose that individual values of BE may provide insight into dispersal behavior (see Oring & Lank 1984). BE may also be useful in gauging the effectiveness of management, such as habitat restoration or restrictions on human activity. It is common to evaluate the success of restoration or effectiveness of mitigating disturbance based on the number of nests in an area (Lafferty *et al.* 2006). In this case, practices may need to be adjusted if such actions attract breeding plovers but they exhibit low BE owing to predation or human disturbance.

In summary, we suggest that BE may be a reasonable substitute for intensive monitoring of individually marked birds to estimate productivity. This may be especially true of plovers and other species that breed in open habitats, where they are easily observed. We urge others to examine this metric and its relationships with PCFS and nest density to provide additional insight into its utility. In particular, the relationship between breeding density and BE may be sensitive to density-dependent predation. In this case, high quality habitat may produce low BE if predators concentrate at sites with large numbers of nests. We urge others who have monitored plovers elsewhere to determine if BE can be generalized to other locations both within the Pacific coast range of the Snowy Plover and worldwide. We suspect, however, that BE may not have utility in monitoring many other species of shorebird in which finding nests, observing incubating adults, and monitoring broods proves more difficult in habitats where vegetation compromises easy detection of breeding individuals, their nests and broods.

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