

LIFE-HISTORY TRAITS AND DIVERGENCE IN POPULATION TRENDS OF TWO NORTH PACIFIC AUKS: RHINOCEROS AUKLET *CERORHINCA MONOCERATA* AND TUFTED PUFFIN *FRATERCULA CIRRHATA*

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ABSTRACT

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Population trends in two closely related and ecologically similar North Pacific auks, the Rhinoceros Auklet *Cerorhinca monocerata* and Tufted Puffin *Fratercula cirrhata*, have diverged over recent decades: stable in the former, declining in the latter. I propose that differences between the two species in a broad suite of interrelated morphological, demographic, behavioral, and physiological life-history traits could explain their differing responses to recent environmental conditions.

Key words: Life-history traits, North Pacific Ocean, population trends, puffins

INTRODUCTION

One issue that has been top of mind at recent gatherings of the Pacific Seabird Group's Tufted Puffin Technical Committee is diverging population trends in two North Pacific auks, the Rhinoceros Auklet *Cerorhinca monocerata* and Tufted Puffin *Fratercula cirrhata*. The two species are more closely related than their names suggest: *Cerorhinca* is thought to be basal to *Fratercula* within the puffin clade (Fraterculini), or the two genera may form sister clades (Smith & Clarke 2015). They also share a broad suite of ecological traits: they are highly colonial; they are generalist feeders; they nest in rock cavities or earthen burrows on predator-free islands; they lay single-egg clutches; and they provision offspring with bill-loads consisting mainly of one-to-many forage fish, including many of the same species (Gaston & Jones 1998). The breeding range of the two species largely overlaps across the North Pacific Ocean, as far south as central California, USA, in the east and northern Japan in the west. However, the Rhinoceros Auklet has a disjointed distribution, being virtually absent as a breeder in the Aleutian Islands and Bering Sea, whereas the Tufted Puffin has a continuous pan-Pacific distribution (Gaston & Jones 1998). The Rhinoceros Auklet is most abundant from the state of Washington, USA, north to southeastern Alaska, USA, in the east (Vermeer 1979) and from Hokkaido, Japan, to the southern Kuril Islands in the west (Ushakova 2007). The Tufted Puffin reaches peak abundance in the eastern Aleutian Islands (Gibson & Byrd 2007).

In the eastern North Pacific, the Tufted Puffin is in marked decline from California to the Gulf of Alaska (Goyert *et al.* 2017, Blight & McLelland 2022, Pearson *et al.* 2023). Its status is listed as Special Concern in California and British Columbia, Canada; as Sensitive in Oregon, USA; and as Endangered in Washington. In the western North Pacific, it has been in decline in Japan since the 1970s—its status was listed as Endangered in 1993 (Osa & Watanuki 2002) and is now nearing extirpation (Internet Nature Institute 2013). In contrast, Rhinoceros Auklet populations appear to be stable

or increasing throughout their range, including in regions where puffins are declining (Slater & Byrd 2009, Rodway & Lemon 2011, Internet Nature Institute 2013, Pearson *et al.* 2013, Bathrick *et al.* 2021). The causes of population decline in Tufted Puffins are poorly understood, although marine pollution, fisheries bycatch, invasive species, and the recovery of Bald Eagles *Haliaeetus leucocephalus* have been invoked (Pearson *et al.* 2023). The fact that the declines are most severe in the south on both sides of the North Pacific Ocean suggests that large-scale climatic phenomena are involved, likely affecting the puffins' long-term reproductive output through prey base perturbation (Hart *et al.* 2018, Pearson *et al.* 2023). However, the evidence from eastern North Pacific colonies where both Rhinoceros Auklets and Tufted Puffins occur suggests that oceanographic variation has similar effects on the prey base of the two species, which overlaps to a large extent—briefly, cold and highly productive is beneficial, warm and unproductive is detrimental (Gjerdrum *et al.* 2003, Borstad *et al.* 2011, Sydeman *et al.* 2017). Why then should their productivity, and ultimately their population trends, diverge in response to that variation?

In a recent paper comparing the biology of ~500-g Rhinoceros Auklets and ~800-g Tufted Puffins on Middleton Island, Alaska, over four years, Shoji *et al.* (2023) concluded by saying: “While auklets have relatively constant breeding success among years at Middleton Island, puffins have a boom-and-bust cycle, with only a few years of high breeding success interspersed by many years of low success.” That conclusion aligns with observations on Triangle Island, British Columbia, in four earlier years (Vermeer & Cullen 1979). Combining the two studies, Rhinoceros Auklets bred more successfully than Tufted Puffins in all eight years, mainly due to consistently higher hatching success (Table 1). [I assume that investigator disturbance was not a confounding factor.] Similarly, between 1995 and 2001 at Triangle Island, fledging success ranged from 53% to 97% in Rhinoceros Auklets (Hedd *et al.* 2006, Borstad *et al.* 2011) but from 0% to 94% in Tufted Puffins (Gjerdrum *et al.* 2003). To explain the interspecific difference, Shoji *et al.* (2023)

TABLE 1
Percentage hatching success (egg-laying to hatching), fledging success (hatching to fledging), and breeding success (egg-laying to fledging) of Rhinoceros Auklets *Cerorhinca monocerata* (RHAU) and Tufted Puffins *Fratercula cirrhata* (TUPU) at Triangle Island, British Columbia, Canada, and at Middleton Island, Alaska, USA, over four years^a

Colony	Year	RHAU			TUPU		
		Hatching success (%)	Fledging success (%)	Breeding success (%)	Hatching success (%)	Fledging success (%)	Breeding success (%)
Triangle	1975	80	73	58	81	57	46
	1976	94	34	32	4	33	1
	1977	91	65	59	53	2	1
	1978	83	83	62	74	74	55
Middleton	2016	63	79	59	32	77	24
	2017	65	75	48	24	71	17
	2018	57	94	54	48	89	42
	2019	72	82	59	33	95	32

^a Data from Vermeer & Cullen (1979) and Shoji *et al.* (2023)

proposed that “high wing-loading and smaller foraging ranges may cause puffins to be more sensitive to prey availability and distribution, whereas auklets forage over larger areas and thus may be able to find food even in years of reduced prey availability.” I agree that morphology (wing-loading) is likely to be a critically important factor, and it appears to be the major factor driving segregation between the two species in their choice of nesting areas on Triangle Island, with Tufted Puffins requiring steeper slopes than Rhinoceros Auklets (Vermeer 1979). I would go a step further and propose that wing-loading is just one central strand within a complex web of interwoven life-history traits that differ between the two species and that could underlie their differing responses to environmental variation. Here, I will consider three life-history traits—one demographic, one behavioral, one physiological—that might combine to play key roles.

Lower vs. higher adult survival rates

Adult survival rates measured on Triangle Island were considerably higher in Tufted Puffins than in Rhinoceros Auklets, ~93% per year vs. ~86% per year for both sexes combined (Morrison *et al.* 2011). With higher adult survival rates, and thus higher residual reproductive value, one should expect puffins to take a more prudent approach to parenting (Drent & Daan 1980), i.e., they should be more likely to forego or abandon a breeding attempt when feeding conditions are poor. Based on Table 1, it appears that Tufted Puffins exhibit a much higher propensity to abandon eggs than do Rhinoceros Auklets. Poor environmental conditions that persist over long periods could ultimately lead to slow population declines, as an extended series of years of low reproductive effort, resulting in low reproductive output, overrides the demographic foundation of a high adult survival rate.

Nocturnal vs. diurnal colony visitation

Vermeer *et al.* (1979) proposed that the nocturnal habits of Rhinoceros Auklets liberate them to expand their foraging range when experiencing poor feeding conditions because, unlike the diurnal puffins, they return to the nest site just once per 24-hour period to exchange incubation duties and provision nestlings. This

obvious constraint (i.e., they can come and go only under cover of darkness, presumably to avoid predators) should lead to greater variation in foraging range, rather than de facto longer foraging range (Shoji *et al.* 2023). In other words, birds will obtain prey close to the colony if possible; if not, they will expand the search area. Vermeer *et al.* (1979) also proposed that crepuscular foraging to collect bill-loads of prey to deliver to the nest might enable Rhinoceros Auklets to access alternative prey types not readily available to puffins provisioning during daylight hours. As an example, Vermeer *et al.* specifically mentioned that Rhinoceros Auklets at Triangle Island delivered the forage fish Pacific Saury *Cololabis saira* to nestlings in many years, especially late in the season after Pacific Sand Lance *Ammodytes personatus*, their primary prey, became unavailable (Hedd *et al.* 2006). Whether this mechanism contributes to differences in the choice of prey at Middleton Island (e.g., more Hexagrammidae greenlings in Rhinoceros Auklet diets, more Pacific Herring *Clupea pallasii* and Prowfish *Zaprora silenus* in Tufted Puffin diets) is an open question (Shoji *et al.* 2023).

Because they deliver prey to the nest during the day, Tufted Puffins are vulnerable at some breeding colonies to kleptoparasitism of their meals by gulls *Larus* spp. (St. Clair *et al.* 2001). Puffins may also have to engage in energetically costly fly-by behaviors to evade the gulls (Blackburn *et al.* 2009).

Slower vs. faster offspring development

Longer developmental periods evolve to minimize costs associated with a limited and/or unpredictable food supply (Cooney *et al.* 2020). In other words, pre-programmed slow growth acts as a buffer against food shortage. In birds, larger species lay larger eggs, and the relationship is stronger at lower levels of taxonomic organization (Rotenberry & Balasubramaniam 2020); it is very strong within the auks (Alcidae; Fig. 1 top and Table 2). Larger eggs are also associated with longer incubation periods among avian species, and this association is again especially evident at lower taxonomic levels (Cooney *et al.* 2020). That no such relationship exists within the auks (Fig. 1 bottom) undoubtedly reflects the unusual degree of variation in nesting habits within the group (Gaston & Jones 1998).

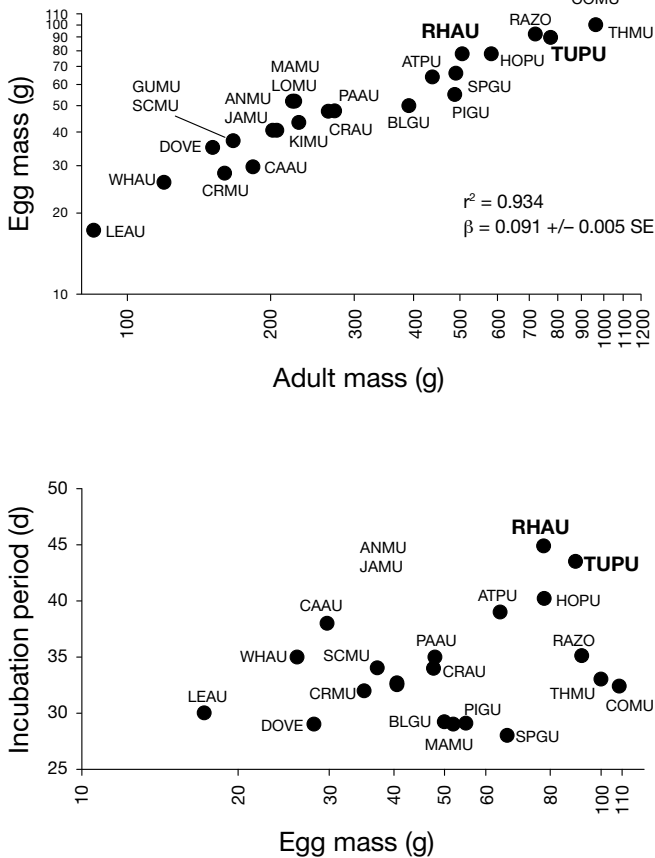


Fig. 1. Egg mass in relation to adult mass (top) and duration of the incubation period in days in relation to egg mass (bottom) in the Alcidae. SE = standard error. For species names, see Table 2. Data from Rotenberry & Balasubramaniam (2020).

As depicted in Fig. 2, shorter incubation periods relative to egg mass in the auks (i.e., relatively faster embryonic development) are associated with using exposed nest sites, as in the Common *Uria aalge* and Thick-billed *U. lomvia* murre. Shorter incubation times are also associated with laying clutches of two eggs rather than one, which introduces competition between siblings to hatch first in order to gain the upper hand, as in the Black *Cepphus grylle*, Pigeon *C. columba*, and Spectacled *C. carbo* guillemots. In contrast, nocturnal habits are associated with longer incubation periods, as in Cassin’s Auklet *Ptychoramphus aleuticus* (Hipfner *et al.* 2010). Note that incubation duration relative to egg mass is substantially longer in the nocturnal Rhinoceros Auklet than in the three diurnal *Fratercula* puffins (Atlantic *F. arctica*, Horned *F. corniculata*, and Tufted puffins; Fig. 2). That this relationship has a physiological basis and is not simply due to more frequent egg neglect (Sealy 1984) is indicated by the fact that the shells of Rhinoceros Auklet eggs are less porous than those of Tufted Puffin eggs (Zimmermann & Hipfner 2007). Low eggshell porosity reduces the embryo’s respiration rate and thus its rate of development, leading to an extended incubation period (Burton & Tullett 1983).

Incubation periods also correlate positively with nestling periods in birds (Lack 1968), presumably due to selection for a constant (uninterrupted) rate of development (Bennett & Owens 2002). Although less tightly constrained than embryonic development and more variable, depending on the amount of food delivered

TABLE 2
Four-letter codes, common names, scientific names for the 24 species of auks

Four-letter code	Common name	Scientific name
ANMU	Ancient Murrelet	<i>Synthliboramphus antiquus</i>
ATPU	Atlantic Puffin	<i>Fratercula arctica</i>
BLGU	Black Guillemot	<i>Cepphus grylle</i>
CAAU	Cassin’s Auklet	<i>Ptychoramphus aleuticus</i>
COMU	Common Murre	<i>Uria aalge</i>
CRAU	Crested Auklet	<i>Aethia cristatella</i>
CRMU	Craveri’s Murrelet	<i>Synthliboramphus craveri</i>
DOVE	Dovekie or Little Auk	<i>Alle alle</i>
GUMU	Guadalupe Murrelet	<i>Synthliboramphus hypoleucus</i>
HOPU	Horned Puffin	<i>Fratercula corniculata</i>
JAMU	Japanese Murrelet	<i>Synthliboramphus wumizusume</i>
KIMU	Kittlitz’s Murrelet	<i>Brachyramphus brevirostris</i>
LEAU	Least Auklet	<i>Aethia pusilla</i>
LOMU	Long-billed Murrelet	<i>Brachyramphus perdix</i>
MAMU	Marbled Murrelet	<i>Brachyramphus marmoratus</i>
PAAU	Parakeet Auklet	<i>Aethia psittacula</i>
PIGU	Pigeon Guillemot	<i>Cepphus columba</i>
RAZO	Razorbill	<i>Alca torda</i>
RHAU	Rhinoceros Auklet	<i>Cerorhinca monocerata</i>
SCMU	Scripps’s Murrelet	<i>Synthliboramphus scrippsi</i>
SPGU	Spectacled Guillemot	<i>Cepphus carbo</i>
THMU	Thick-billed Murre	<i>Uria lomvia</i>
TUPU	Tufted Puffin	<i>Fratercula cirrhata</i>
WHAU	Whiskered Auklet	<i>Aethia pygmaea</i>

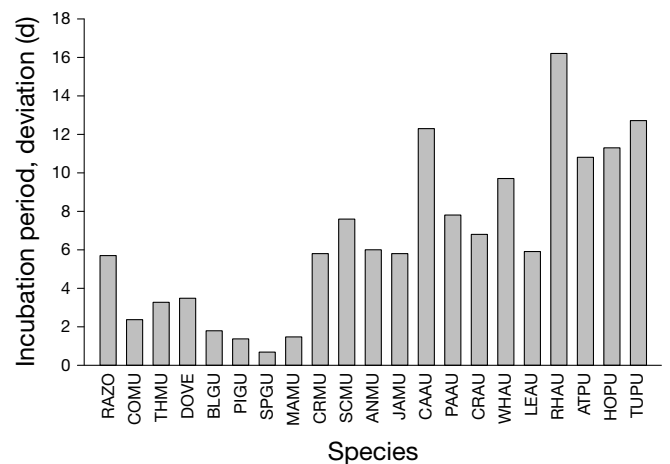


Fig. 2. Deviation from values expected from egg mass in the duration of incubation periods (in days) in the Alcidae in relation to a Charadriiformes baseline using the formula in Cooney *et al.* (2020). For species names see Table 2.

by parents to their offspring (Starck 1998), the duration of post-embryonic development in the nest also tends to be longer in the smaller Rhinoceros Auklet (> 50 days) than in the larger Tufted Puffin (< 45 days) in the same environment (Vermeer & Cullen 1979). Again, nocturnal (one feed per parent per day) vs. diurnal (multiple feeds per parent per day) provisioning is a key factor in the rate of chick development (Vermeer & Cullen 1979).

The end result is that the Rhinoceros Auklet, despite having a smaller egg, a smaller nestling, and a smaller fledgling, typically takes ~6–8 days longer than the Tufted Puffin to get from egg-laying to fledging. That slower development presumably enhances the offspring's capacity to survive periods of food shortage while in the nest (Cooney *et al.* 2020). Or as Vermeer & Cullen (1979) stated: "The fact that [Rhinoceros Auklet nestlings] nevertheless fledged [in years of poor food supply] indicates their adaptiveness to adverse circumstances [relative to Tufted Puffin nestlings]." Wagner *et al.* (2023) also suggested that Rhinoceros Auklets exhibited more resiliency than other seabirds to a severe marine heatwave (The Blob; Bond *et al.* 2015). This hypothesis offers an explanation for why Tufted Puffins appear to be more likely than Rhinoceros Auklets to abandon offspring, and particularly eggs (Table 1): with higher adult survival rates and with offspring that lack the equivalent capacity to slow post-hatching growth in response to food shortage, puffins may be more likely to terminate breeding ahead of the energetically demanding provisioning stage if and when environmental cues indicate that feeding conditions will not be adequate to make the attempt worthwhile. Raising the bar even higher, Tufted Puffins that fledged at heavier mass and with longer wings were more likely to survive after fledging (Morrison *et al.* 2009), but no comparison with Rhinoceros Auklets is possible because post-fledging survival has not been studied in that species.

CONCLUSIONS

Adverse environmental conditions could impact sympatric species of seabirds differently, depending on specifics of their life histories (Strong & Duarte 2023, Woehler & Hobday 2023). The analysis presented here, combined with those of Vermeer & Cullen (1979) and Shoji *et al.* (2023), suggests that a complex web of morphological, demographic, behavioral, and physiological traits interact to set a lower ceiling on parental investment and a lower floor at which to terminate breeding for Tufted Puffins compared to Rhinoceros Auklets. Adverse environmental conditions have often prevailed in the eastern North Pacific Ocean over recent decades, including a recent series of dramatic marine heatwaves that caused unprecedented seabird die-offs (Jones *et al.* 2018, 2019; Piatt *et al.* 2020). I propose that divergence in population trends in these two species of North Pacific puffins over recent decades could be a consequence of Rhinoceros Auklets having greater and Tufted Puffins having lesser resilience to environmental perturbation while breeding.

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REFERENCES

- BATHRICK, R., BECK, J., CARLE, R. & HESTER, M. 2021. *Año Nuevo State Park Seabird Conservation and Habitat Restoration: 2020*. Unpublished report. Sacramento, USA: California Department of Parks and Recreation, Año Nuevo State Park.
- BENNETT, P.M. & OWENS, I.P.F. 2002. *Evolutionary Ecology of Birds: Life Histories, Mating Systems, and Extinction*. Oxford, UK: Oxford University Press.
- BLACKBURN, G.S., HIPFNER, J.M. & YDENBERG, R.C. 2009. Evidence that Tufted Puffins *Fratercula cirrhata* use colony overflights to reduce kleptoparasitism risk. *Journal of Avian Biology* 40: 412–418.
- BLIGHT, L.K. & MCCLELLAND, G. 2022. Historical distribution and current population status of Tufted Puffins *Fratercula cirrhata* in Canada's California Current System. *Marine Ornithology* 50: 35–42.
- BOND, N.A., CRONIN, M.F., FREELAND, H. & MANTUA, N. 2015. Causes and impacts of the 2014 warm anomaly in the NE Pacific. *Geophysical Research Letters* 42: 3414–3420.
- BORSTAD, G., CRAWFORD, W., HIPFNER, J.M., THOMSON, R. & HYATT, K. 2011. Environmental control of the breeding success of Rhinoceros Auklets at Triangle Island, British Columbia. *Marine Ecology Progress Series* 424: 285–302. doi:10.3354/meps08950
- BURTON, F.G. & TULLET, S.G. 1983. A comparison of the effects of eggshell porosity on the respiration and growth of domestic fowl, duck and turkey embryos. *Comparative Biochemistry and Physiology, Part A* 75: 167–174.
- COONEY, C.R., SHEARD, C., CLARK, A.D., ET AL. 2020. Ecology and allometry predict the evolution of avian developmental durations. *Nature Communications* 11: 2383. doi:10.1038/s41467-020-16257-x
- DRENT, R.H. & DAAN, S. 1980. The prudent parent: Energetic adjustments in avian breeding. *Ardea* 68: 225–252.
- GASTON, A.J. & JONES, I.L. 1998. *The Auks: Alcidae*. Oxford, UK: Oxford University Press.
- GIBSON, D.D. & BYRD, G.V. 2007. *Birds of the Aleutian Islands, Alaska*. Cambridge, UK: Nuttall Ornithological Club; Washington, USA: American Ornithologists' Union.
- GJERDRUM, C., VALLEE, A.M.J., ST. CLAIR, C.C., BERTRAM, D.F., RYDER, J.L. & BLACKBURN, G.S. 2003. Tufted Puffin reproduction reveals ocean climate variability. *Proceedings of the National Academy of Sciences* 100: 9377–9382.
- GOYERT, H.F., GARTON, E.O., DRUMMOND, B.A. & RENNER, H.M. 2017. Density dependence and changes in the carrying capacity of Alaskan seabird populations. *Biological Conservation* 209: 178–187. doi:10.1016/j.biocon.2017.02.011
- HART, C.J., KELLY, R.P. & PEARSON, S.F. 2018. Will the California Current lose its nesting Tufted Puffins? *PeerJ* 6: e4519. doi:10.7717/peerj.4519
- HEDD, A., BERTRAM, D.F., RYDER, J.L. & JONES, I.L. 2006. Effects of interdecadal climate variability on marine trophic interactions: Rhinoceros Auklets and their fish prey. *Marine Ecology Progress Series* 309: 263–278. doi:10.3354/meps309263.
- HIPFNER, J.M., GORMAN, K.B., VOS, R.A. & JOY, J.B. 2010. Evolution of embryonic developmental period in the marine bird families Alcidae and Spheniscidae: Roles for nutrition and predation? *BMC Evolutionary Biology* 10: 179. doi:10.1186/1471-2148-10-179

- INTERNET NATURE INSTITUTE. 2013. *Japanese Seabird Colony Database*. Tokyo, Japan: Ministry of the Environment, Biodiversity Center of Japan. [Accessed at <https://www.sizenken.biodic.go.jp/seabirds/> on 10 October 2023.]
- JONES, T., DIVINE, L.M., RENNER, H., ET AL. 2019. Unusual mortality of Tufted puffins (*Fratercula cirrhata*) in the eastern Bering Sea. *PLoS One* 14: e0216532.
- JONES, T., PARRISH, J.K., PETERSON, W.T., ET AL. 2018. Massive mortality of a planktivorous seabird in response to a marine heatwave. *Geophysical Research Letters* 45: 3193–3202. doi:10.1002/2017GL076164
- LACK, D. 1968. *Ecological Adaptations for Breeding in Birds*. London, England: Methuen.
- MORRISON, K.W., HIPFNER, J.M., BLACKBURN, G.S. & GREEN, D.J. 2011. Effects of extreme climate events on adult survival of three Pacific auks. *The Auk* 128: 707–715. doi:10.1525/auk.2011.10198
- MORRISON, K.W., HIPFNER, J.M., GJERDRUM, C. & GREEN, D.J. 2009. Wing length and mass at fledging predict local juvenile survival and age at first return in Tufted Puffins. *The Condor* 111: 433–441. doi:10.1525/cond.2009.080099
- OSA, Y. & WATANUKI, Y. 2002. Status of seabirds breeding in Hokkaido. *Journal of the Yamashina Institute for Ornithology* 33: 107–141. doi:10.3312/jyio1952.33.107
- PEARSON, S.F., HODUM, P.J., GOOD, T.P., SCHRIMPF, M. & KNAPP, S.M. 2013. A model approach for estimating colony size, trends, and habitat associations of burrow-nesting seabirds. *The Condor* 115: 356–365. doi:10.1525/cond.2013.110207
- PEARSON, S.F., KEREN, I., HODUM, P.J., ET AL. 2023. Range-wide changes in the North American Tufted Puffin *Fratercula cirrhata* breeding population over 115 years. *Bird Conservation International* 33: e24. doi:10.1017/S0959270922000193
- PIATT, J.F., PARRISH, J.K., RENNER, H.M., ET AL. 2020. Extreme mortality and reproductive failure of Common Murres resulting from the Northeast Pacific marine heatwave of 2014–2016. *PLoS One* 15: e0226087.
- RODWAY, M.S. & LEMON, M.J.F. 2011. Use of permanent plots to monitor trends in burrow-nesting seabird populations in British Columbia. *Marine Ornithology* 39: 243–253.
- ROTENBERRY, J.T. & BALASUBRAMANIAM, P. 2020. Estimating egg mass–body mass relationships in birds. *The Auk* 137: ukaa019. doi:10.1093/auk/ukaa019
- SEALY, S.G. 1984. Interruptions extend incubation by Ancient Murrelets, Crested Auklets, and Least Auklets. *The Murrelet* 65: 53–56. doi:10.2307/3535298
- SHOJI, A., WHELAN, S., CUNNINGHAM, J.T., ET AL. 2023. Ecological niche partitioning in two Pacific puffins. *Marine Ecology Progress Series* 709: 125–139. doi:10.3354/meps14282
- SLATER, L. & BYRD, G.V. 2009. Status, trends, and patterns of covariation of breeding seabirds at St. Lazaria Island, southeast Alaska, 1994–2006. *Journal of Biogeography* 36: 465–475.
- SMITH, N.A. & CLARKE, J.A. 2015. Systematics and evolution of the Pan-Alcidae (Aves, Charadriiformes). *Journal of Avian Biology* 46: 125–140. doi:10.1111/jav.00487
- ST. CLAIR, C.C., ST. CLAIR, R.C. & WILLIAMS, T.D. 2001. Does kleptoparasitism by Glaucous-winged Gulls limit the reproductive success of Tufted Puffins? *The Auk* 118: 934–943.
- STARCK, J.M. 1998. Structural variants and invariants in avian embryonic and postnatal development. In: STARCK, J.M. & RICKLEFS, R.E. (Eds.) *Avian Growth and Development: Evolution within the Altricial–Precocial Spectrum*. London, England: Oxford University Press.
- STRONG, C.S. & DUARTE, A. 2023. Reproductive indices of Common Murres *Uria aalge* and Marbled Murrelets *Brachyramphus marmoratus* indicate murrelets are more resilient during poor years. *Marine Ornithology* 51: 187–194.
- SYDEMAN, W.J., PIATT, J.F., THOMPSON, S.A., ET AL. 2017. Puffins reveal contrasting relationships between forage fish and ocean climate in the North Pacific. *Fisheries Oceanography* 26: 379–395. doi:10.1111/fog.12204
- USHAKOVA, M.V. 2007. The Rhinoceros Auklet (*Cerorhinca monocerata*, Alcidae) colonies and number on the southern Kuril Islands. *Zoologicheskii Zhurnal* 86(8): 955–965. (English abstract)
- VERMEER, K. 1979. Nesting requirements, food and breeding distribution of Rhinoceros Auklets, *Cerorhinca monocerata* and Tufted Puffins *Lunda cirrhata*. *Ardea* 67: 101–110.
- VERMEER, K. & CULLEN, L. 1979. Growth of Rhinoceros Auklets and Tufted Puffins, Triangle Island, British Columbia. *Ardea* 67: 22–27.
- VERMEER, K., CULLEN, L. & PORTER, M. 1979. A provisional explanation of the reproductive failure of Tufted Puffins *Lunda cirrhata* on Triangle Island, British Columbia. *Ibis* 121: 348–354.
- WAGNER, E.L., PEARSON, S.F., GOOD, T.P., HODUM, P.J., BUHLE, E.R. & SCHRIMPF, M.B. 2023. Resilience to a severe marine heatwave at two Pacific seabird colonies. *Marine Ecology Progress Series* 737: 101–120. doi:10.3354/meps14222
- WOEHLER, E.J. & HOBDAJ, A.J. 2023. Impacts of marine heatwaves may be mediated by seabird life history strategies. *Marine Ecology Progress Series* 737: 9–23. doi:10.3354/meps14333
- ZIMMERMANN, K. & HIPFNER, J.M. 2007. Egg size, eggshell porosity, and incubation period in the marine bird family Alcidae. *The Auk* 124: 307–315.