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RESEARCH ARTICLE

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Feeding trial evaluation of supplemental sodium and calcium use by pigeons

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Abstract

The Pacific Coast band-tailed pigeon's (*Patagioenas fasciata monilis*) conspicuous and well documented use of supplemental minerals has allowed wildlife managers to conduct counts of pigeons at sites with minerals to index their abundance; but despite at least 9 associated peer-reviewed research publications since 1998, the reason that band-tailed pigeons use mineral sites and necessity of that use remains unknown. I conducted feeding trials with pigeons during summers of 2009 and 2010 to evaluate maintenance and reproductive performance associated with access to supplemental minerals: one with 24 pairs of wild-caught band-tailed pigeons, and one with 30 pairs of wild-caught rock pigeons (*Columba livia*). Data indicate that red elderberry (*Sambucus racemosa var. arborescens*) and cascara (*Rhamnus purshiana*) berries (natural food items) are high energy food sources for band-tailed pigeons, and that band-tailed pigeons can thrive on these berries without access to supplemental sodium and calcium. However, access to supplemental sodium could offer band-tailed pigeons advantages in body weight maintenance or gain when consuming a diet low in sodium and high in potassium. Band-tailed pigeons did not nest in this study; thus, it remains unknown if there are benefits to reproductive performance from access to supplemental minerals. Rock pigeons with access to supplemental sodium fledged ≥33% more young than those pigeons without access to supplemental sodium, and this

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was primarily associated with the increased number of clutches and increased fledging rate. Also, fledgling mass was greater ($\bar{x}$ ± SE = 35.5 ± 7.9 g, 95% CI = 19.3–51.8) for rock pigeons with access to supplemental sodium at fledging in 2010, but the difference was not statistically significant in 2009 (5.9 ± 22.9, 95% CI = − 43.2–55.0) possibly because of the nutritionally limited diet that year. Access to supplemental sodium could offer band-tailed pigeons advantages in fecundity and hatchling survival rates (recruitment) through increased efficiency in food conversion. Natural mineral sites used by band-tailed pigeons should be conserved until additional information is available for evaluation. Also, comparison of counts of band-tailed pigeons at mineral sites over time and among sites must be interpreted cautiously until the factors (e.g., diet, weather, accessibility, supplemental mineral concentration, etc.) that influence the proportion of the local band-tailed pigeon population that uses mineral sites can be determined.

KEYWORDS

band-tailed pigeon, calcium, *Columba livia*, feeding trial, mineral site, *Patagioenas fasciata*, rock pigeon, salt, sodium, supplemental mineral use

Pacific Coast band-tailed pigeons (*Patagioenas fasciata monilis*) congregate at and use mineral sites (mineralized water or soil) primarily within their breeding range, but interior band-tailed pigeons (*P. f. fasciata*) generally do not exhibit this behavior (Sanders and Braun 2022). The band-tailed pigeon's use of supplemental minerals has been the focus of at least 9 peer reviewed research publications since 1998 following earlier work in 1947, 1968–1975, and 1992 (Table 1). Since 1998, following long-term negative trends in band-tailed pigeon abundance (U.S. Fish and Wildlife Service [USFWS] 2020), research on band-tailed pigeon use of supplemental mineral sites was motivated by implications for conservation of the species and monitoring species abundance. Supplemental mineral sites were thought to be a critical resource for Pacific Coast band-tailed pigeon maintenance and reproduction in the northwestern U.S. where they consume fruits, primarily elderberry berries (March and Sadleir 1972, 1975; Jarvis and Passmore 1992; Braun 1994), and thus counts at mineral sites could be used as an unbiased index of abundance (Casazza et al. 2005, USFWS 2020).

Subsequent research indicates the ion sought at mineral sites is sodium (Sanders and Jarvis 2000, Sanders and Koch 2018) but was previously thought to be calcium (March and Sadleir 1972, 1975; Jarvis and Passmore 1992; Braun 1994). Sanders and Koch (2018) determined that band-tailed pigeons visited a supplemental sodium site on average once every 12 days (but individual pigeons ranged from 1 to 2 week intervals between visits) during June through early October in Washington, USA. Males arrive and depart supplemental mineral sites between daylight and 1000 hours and females between 0930 and 1200 hours, the inverse of the nest attentive schedules for the sexes (Jarvis and Passmore 1992, Sanders and Koch 2018). Use of supplemental sodium during the breeding season by Pacific Coast band-tailed pigeons has been associated with egg and crop milk production and may be increased by a berry diet low in sodium and high in moisture and potassium content (Sanders and Jarvis 2000, Sanders and Koch 2018).

TABLE 1 Peer reviewed research publications on the band-tailed pigeon's (*Patagioenas fasciata*) use of supplemental minerals.

Author	Year	Contribution toward understanding supplemental mineral use
Neff	1947	Habits, food, and economic status of the band-tailed pigeon with reference to observations of pigeon use of mineral sites in the Pacific Coast region
Smith	1968	Mineral content of 2 mineral sites in northern California used by pigeons
March and Sadleir	1972	Mineral content of 11 mineral sites in Oregon, Washington, and British Columbia used by pigeons
March and Sadleir	1975	Seasonal changes in body weight and calcium distribution during the breeding season
Jarvis and Passmore	1992	Daily mineral site use patterns and association with food items during the nesting season in western Oregon; patagial tag-marked pigeons
Leonard	1998	Nesting and foraging ecology of band-tailed pigeons in western Oregon, including consideration of mineral site use; VHF radio-marked pigeons
Sanders and Jarvis	2000	Mineral content of all mineral sites ($n = 65$) known to be used by pigeons in western Oregon
Sanders and Jarvis	2003	Associations of pigeons and nests with mineral site distribution in western Oregon; pigeon counts and VHF radio-marked pigeon data
Casazza et al.	2005	Evaluation of population indices for power to detect trends in pigeon count data at mineral sites; pigeon counts
Overton et al.	2005	Post-precipitation bias in counts at mineral sites; pigeon counts
Overton et al.		Linking landscape characteristics to mineral site use
Overton et al.	2006, 2010	Scale-dependent associations of pigeon counts at mineral sites
Sanders and Koch	2018	Pigeon use of a mineral site in SW Washington; Passive Integrated Transponder-marked pigeons
Sanders and Braun	2022	Minerals in gastroliths and foods consumed by pigeons in the Interior and Pacific Coast regions

Supplemental sodium could be a critical resource when band-tailed pigeons feed on berries during the breeding season in the Pacific Northwest because the birds may be deficient in sodium and may have a sodium and potassium cation electrolyte imbalance (Sanders and Jarvis 2000). However, use of supplemental sodium can occur year around (Sanders and Koch 2018). Band-tailed pigeons are ubiquitous across habitats in the Pacific Northwest regardless of distance to supplemental mineral sites (Sanders and Jarvis 2003), and some pigeons do not use supplemental mineral sites (Sanders and Koch 2018). Band-tailed pigeons in the interior region of the U.S. (Colorado, Utah, Arizona, and New Mexico) do not use supplemental mineral sites to any extent despite a similar diet high in potassium and low in sodium (Sanders and Braun 2022). The band-tailed pigeons' use of supplemental mineral sites in part of their range is not well explained by minerals in grit or minerals and moisture in food items consumed (Sanders and Braun 2022).

The proportion of the Pacific Coast band-tailed pigeon population that uses supplemental mineral sites remains unknown. Understanding why band-tailed pigeons use mineral sites (e.g., how necessity and frequency of use may vary in time and space depending on environmental factors) has implications for interpreting counts of pigeons at these sites in current monitoring programs (USFWS 2020) and understanding if mineral availability from grit or water and mineral sites limit pigeon productivity, population size, and distribution (Keppie and Braun 2000).

My objective was to examine the potential benefits in pigeon maintenance and reproduction associated with pigeon use of supplemental minerals. I hypothesized that pigeons without access to supplemental mineral would be unable to maintain health (evidenced by loss in mass and mortality) and reproductive performance (evidenced by reduced fecundity, fledgling mass) when consuming some natural berry species commonly available during the breeding season (i.e., supplemental mineral use is necessary or beneficial). This may in part explain why some pigeons, particularly those in the Pacific Northwest, frequent mineral sites for supplemental sodium during the breeding season.

STUDY AREA

My study area included a privately owned forest (3.0 ha) in southwestern Washington, USA, approximately 8 km east southeast of Battle Ground at 150 m elevation in the mountainous foothills of the western Cascade Range (24 km north of the Oregon and Washington state border). The study area occurred near the center of the breeding range of Pacific Coast band-tailed pigeons and the distribution of mineral sites used by these birds. Climate was marine west coast, characterized by wet, mild winters (Oct–Jun), and cool, dry summers (Jul–Sep) with abundant rainfall (100–200 cm), 75–85% of which occurred between 1 October and 31 March in the form of rain (Franklin and Dyrness 1973, Loy et al. 1976). The study area was the same study area used and described by Sanders and Koch (2018).

METHODS

I conducted feeding trials with pigeons during summer 2009 and 2010 to evaluate maintenance and reproductive performance associated with access to supplemental minerals: one with 24 pairs of wild-caught band-tailed pigeons, and one with 30 pairs of wild-caught rock pigeons (*Columba livia*). I was primarily interested in band-tailed pigeons feeding on natural berry food items but included grain food items when berries were not available. I included rock pigeons assuming that recent-captured wild band-tailed pigeons may not reproduce in captivity as desired for evaluation of supplemental mineral use during reproductive activities.

Band-tailed pigeons

I captured 48 band-tailed pigeons with a drop trap baited with cracked corn (*Zea mays)* in late May–early June 2009 near Battle Ground, WA, for use in feeding trials in both 2009 and 2010. I marked each pigeon with a unique numbered aluminum butt-end leg band (size 5) provided by the U.S. Geological Survey Bird Banding Laboratory (banding permit 23678). The sex of each bird was initially determined by plumage examination (White and Braun 1978, Sanders and Braun 2013) and subsequently verified by blood samples from toenail clipping submitted to Zoogen DNA Services (Davis, CA, USA) for Polymerase Chain Reaction analysis of the DNA from the sex chromosomes of each bird. Pigeons were kept equally distributed between 2 covered outdoor flight cages (2.4 × 1.5 × 1.5 m [LWH]) when not involved in feeding trials. Food and fresh water were provided *ad libitum*. Ample perches were provided and the cage was half surrounded with green shade cloth to minimize disturbance.

Feeding trial cages were self-made 122 × 81 × 152 cm (LWH) of 14 gauge 2.5 × 2.5 cm galvanized welded wire mesh and with a removable dropping tray. Each cage had a similar wire mesh loft and plastic nest bowl with pad, 2 perches (each ~5 cm diameter conifer tree limbs across the width of the cage), and 3 spill proof plastic containers: one for feed, one for fresh water, and one for mineral solution. Mineral solution and water containers were maintained in the same position both years. Cages were adjacent to each other in 2 rows of 6 in back-to-back sets

of 2 with a walking isle between rows. Cages were in an open-sided, covered pole barn near the capture site (Figure 1). Cages and droppings trays were cleaned only as needed during trials to minimize disturbance, but food and water trays were replaced at least biweekly with sterilized replacements. Pigeon pairs were offered an unlimited amount of food, water, and mineral solution and serviced daily.

The feeding trial each year consisted of randomly assigning one male and one female to a cage (experimental unit, $n = 24$) each year, randomly assigning each pair access to 1 of 4 different mineral solutions (treatments, $n = 6$ each), and feeding each pair the same diet for 3–16 consecutive weeks (subtrials) for a total of 15 consecutive weeks (18 Jun–1 Oct) in 2009 and 25 consecutive weeks (27 Mar–19 Sep) in 2010 (Table 2). Pigeons were provided *ad-libitum* fresh tap water, mineral solution, and red elderberry (*Sambucus racemosa* var. *arborescens*) or cascara (*Rhamnus purshiana*) berries, the primary natural foods consumed by these birds during the breeding season in the Pacific Northwest (Jarvis and Passmore 1992, Sanders and Jarvis 2000, Sanders and Braun 2022), and consistent with the timing of berry availability in the region. We provided commercially available grains for the first subtrial each year until fresh berries were available based on plant phenology. Pigeons are known to use grain during early spring in the Pacific Northwest before berries are available. The feeding trial food items (berries and grains) contain



FIGURE 1 Pacific band-tailed (*Patagioenas fasciata monilis*) and rock (*Columba livia*) pigeons feeding trial cages in an open-sided, covered pole barn in Battle Ground, WA, USA, 2009 and 2010.

TABLE 2 Foods and mineral solutions provided to Pacific band-tailed (*Patagioenas fasciata monilis*) and rock (*Columba livia*) pigeons during feeding trials in Battle Ground, WA, USA, 2009 and 2010. Foods included cracked corn (CC, *Zea mays*) Fancier's Choice (FC), red elderberry berries (RE, *Sambucus racemosa* var. *arborescens*), and Cascara berries (CA, *Rhamnus purshiana*). Mineral solutions included sodium chloride at 3,500 ppm sodium concentration (Na), calcium chloride at 1,500 ppm calcium concentration (Ca), sodium chloride and calcium chloride solution at 3,500 ppm sodium and 1,500 ppm calcium concentrations (NaCa), and water with no added minerals (H_2O).

Species	Trial	Subtrial	Period	Days	Food	Mineral[a]	*n*[b]
Band-tailed pigeon	2009	Total	18 Jun–1 Oct	106		Na, Ca, NaCa, H_2O	6
	2009	1	18 Jun–8 Jul	21	CC	Na, Ca, NaCa, H_2O	6
	2009	2	9 Jul–5 Aug	28	RE	Na, Ca, NaCa, H_2O	6
	2009	3	6 Aug–2 Sep	28	CA	Na, Ca, NaCa, H_2O	6
	2009	4	3 Sep–1 Oct	29	RE	Na, Ca, NaCa, H_2O	6
	2010 A	Total	27 Mar–19 Sep	177		Na, H_2O	6
	2010 A	5	27 Mar–17 Jul	113	FC	Na, H_2O	6
	2010 A	6	18 Jul–27 Aug	41	RE	Na, H_2O	6
	2010 A	7	28 Aug–19 Sep	23	CA	Na, H_2O	6
	2010 B	8	27 Mar–19 Sep	177	FC	Na, H_2O	6
Rock pigeon	2009	Total	27 Jun–15 Aug	50	CC	Na, Ca, NaCa, H_2O	7–8[c]
	2010	Total	3 Apr–22 Aug	142	FC	Na, H_2O	15

[a]In 2010, all pairs were provided unlimited access to commercially available flint grit (insoluble Cherrystone Grit made from crushed 100% quartzite rock, small No. 1, similar in size to that found in necropsied birds) and oyster shell (calcium) grit.

[b]Number of cages (pairs) per mineral treatment group ($N = 24$ band-tailed pigeons, and $N = 30$ rock pigeons).

[c]Number of cages (pairs) per mineral treatment for H_2O and Na treatment groups was 7 each in 2009 for a total of 30 rock pigeon pairs.

low concentrations of sodium (0.002–0.025%) and high concentrations of potassium (0.31–2.70%) (Sanders and Jarvis 2000, Sanders and Braun 2022).

Mineral solution treatments were in tap water; either sodium, calcium, both (sodium and calcium), or no mineral (water only, control group). The mineral solution for each treatment group was sodium chloride solution at 3,500 ppm sodium concentration, calcium chloride solution at 1,500 ppm calcium concentration, sodium chloride and calcium chloride solution at 3,500 ppm sodium, and 1,500 ppm calcium concentrations, or tap water. Sodium and calcium solutions were similar in concentration to the mean of mineral springs used by band-tailed pigeons in Oregon (Sanders and Jarvis 2000).

Berries provided to pigeons during subtrials were wild picked in Oregon and Washington, fresh frozen, and provided fresh or thawed just prior to feeding. Berries were kept ≤3 months. Band-tailed pigeon pairs were provided about 500 g of fresh or previously frozen berries daily, and generally consumed about 240–375 g per day. Red elderberry and cascara berries were submitted in 2 subsamples each to the Forage Testing Laboratory at Dairy One, Inc. (Ithaca, NY, USA) for proximate analysis of macronutrients (Table 3). Sanders and Jarvis (2000) estimated berry mineral concentrations ($n = 10$ each). Grains were purchased commercially and included cracked corn (Grainland Select, Purina Animal Nutrition, Arden Hills, MN, USA; guaranteed analysis 7% adjusted crude protein, 3.0% crude fiber, 2.5% crude fat, and 0.01–0.06% sodium) and Fancier's Choice, a non-medicated mixed grain fed formulated for pigeons (Land O'Lakes, Inc., Arden Hills, MN, USA; guaranteed analysis 17% adjusted crude protein, 7.5% crude fiber, 6.0% crude fat, 0.06% calcium and 0.004% sodium). I submitted 5 samples of each commercial

TABLE 3 Proximate and mineral analysis of food items provided to Pacific band-tailed (*Patagioenas fasciata monilis*) and rock (*Columba livia*) pigeons during feeding trials in Battle Ground, WA, USA, 2009 and 2010. Food items included cracked corn (CC, *Zea mays*), Fancier's Choice (FC), red elderberry berries (RE, *Sambucus racemosa* var. *arborescens*), and Cascara berries (CA; *Rhamnus purshiana*).

	CC[a]		FC[a]		RE[b]		CA[b]	
Attribute	**Estimate**	**SE**	**Estimate**	**SE**	**Estimate**	**SE**	**Estimate**	**SE**
Water (%)	14.0	0.8	10.3	0.2	76.0	1.1	71.5	0.8
Dry matter (%)	86.0	0.8	89.7	0.2	24.0	1.1	28.5	0.8
Organic (%)	98.0	†[c]	†	†	94.6	0.1	96.8	0.1
Adj. crude protein	7.0	†	17.0	†	11.4	3.1	10.8	1.5
Crude fiber	3.0	†	7.5	†	19.8	6.3	17.0	1.0
Crude fat	2.5	†	6.0	†	23.0	14.8	21.6	11.6
Gross energy[d]	†	†	†	†	5,910	826	6,024	405
Inorganic (%)	2.0	†	†	†	5.4	0.1	3.2	0.1
Calcium (%)	0.024	0.003	0.064	0.002	0.196	0.016	0.229	0.015
Potassium (%)	0.308	0.018	0.626	0.008	2.698	0.109	1.247	0.041
Sodium (%)	0.003	0.001	0.004	<0.001	0.025	0.003	0.002	<0.001

[a]Cracked corn and Fancier's Choice were commercially available food items and macronutrients were provided via manufacturer guarantee analysis. Mineral concentrations were estimated from 5 samples of each commercial food item submitted to the Forage Testing Laboratory at Dairy One for analysis of cation composition by induction-coupled plasma (ICP) spectrometer scan.

[b]Red elderberry and cascara berries were submitted in 2 subsamples each to the Forage Testing Laboratory at Dairy One, Inc. (Ithaca, NY) for proximate analysis of macronutrients. Sanders and Jarvis (2000) estimated moisture, ash, and mineral concentrations ($n = 10$ each).

[c]Estimate not available.

[d]Calories per gram dry matter.

food item to the Forage Testing Laboratory at Dairy One for analysis of cation composition by induction-coupled plasma (ICP) spectrometer scan to verify calcium, potassium, and sodium concentrations (Table 3). Outside of feeding trials (i.e., overwinter), I provided pigeons Fancier's Choice feed and water *ad libitum*.

For feeding subtrials in 2009, I provided pigeons cracked corn for 3 weeks followed by berries of red elderberry for 4 weeks, cascara for 4 weeks, and red elderberry again for 4 more weeks (15 consecutive weeks; Table 2). I had originally intended to feed pigeons berries of blue elderberry (*Sambucus cerulea*) during the last 4 weeks of feeding trials to simulate the natural progression of primary food item availability and use in the Pacific Northwest, but there was little that could be located in the local area. In 2010, I provided Fancier's Choice for 16 weeks and berries of red elderberry for 6 weeks and cascara for 3 weeks (25 consecutive weeks). I started the feeding trial in 2010 with Fancier's Choice because it was a more nutritionally complete diet than cracked corn and what pigeons were provided outside of feeding trials. Only 12 pairs of pigeons were provided berries during berry subtrials in 2010 due to the challenge of locating and picking berries, the other 12 pairs continued to be provided Fancier's Choice.

Pigeons were weighed midday at the beginning and end of each subtrial to the nearest 100th gram on an outdoor scale (Ohaus Adventurer Pro, 810 g max, 0.01 g precision) protected from the wind. I recorded nesting activities to evaluate fecundity and reproductive success. I measured mineral solution consumption weekly to the nearest ml in a graduated cylinder. Evaporation was accounted for in control containers similar to those used for solutions in trials. I measured evaporation weekly in 4 spill-proof plastic containers placed adjacent to the cages and

protected from animal access. I also accounted for measured quantities added as needed during the week to maintain containers at full service level.

After the 2009 subtrials, treatment groups were reduced to sodium chloride solution at 3,500 ppm sodium concentration (Na) or tap water (control) because there was little evidence that reproductive success, fluid (total and mineral solution) consumption, or change in pigeon mass differed between water and calcium treatment groups or between sodium and sodium-calcium treatment groups for both band-tailed pigeon and rock pigeon feeding trials. This decision was also based on the findings of Sanders and Koch (2018), a study conducted at the same time as the feeding trials that determined pigeons seek supplemental sodium and not calcium at mineral sites in the Pacific Northwest. All pairs were provided unlimited access to treatment mineral solution, water, and commercially available flint grit (insoluble Cherrystone Grit made from crushed 100% quartzite rock, small No. 1, similar in size to that found in necropsied birds) and oyster shell (calcium) grit. Sodium solution consumption was measured in 2010, however, fresh water consumption was not.

Rock pigeons

Wild rock pigeons were captured in May 2009 in westcentral Washington by the U.S. Department of Agriculture, Animal and Plant Health Inspection Service, Wildlife Services (Olympia) and provided for use in feeding trials in both 2009 and 2010. Similar to the band-tailed pigeons, I marked each pigeon with a unique numbered aluminum butt-end leg band (size 5; obtained directly from National Band and Tag Company, Newport, KY, USA, for use on nonmigratory birds), and the sex of each bird was assigned based on blood samples from toenail clipping submitted to Zoogen DNA Services (Davis, CA, USA) for DNA analysis. Pigeons were kept equally distributed between 2 covered, outdoor flight cages when not involved in feeding trials. Holding cages were similar to those used to keep band-tailed pigeons outside of feeding trials.

Feeding trial cages were purchased from Quality Cage Company in Portland, OR, USA, and were 61 × 76 × 61 cm (LWH) made of 14 gauge 2.5 × 2.5 cm galvanized welded wire mesh with a removable dropping tray. Each cage had a similar wire mesh loft and plastic nest bowl with pad, and 3 spill-proof plastic containers: one for food, one for fresh water, and one for mineral solution. Cages were adjacent to each other in 2 back-to-back rows of cages (stacked 2 or 3 high) with a walking isle between rows in an open-sided covered pole barn (Figure 1). Cages and droppings trays were cleaned only as needed during trials to minimize disturbance, but food and water trays were replaced at least bi-weekly with sterilized replacements. Pigeon pairs were offered an unlimited amount of feed, water, and mineral solution and serviced daily.

The feeding trial design was the same as that for band-tailed pigeons, except that rock pigeons were fed only cracked corn in 2009 and only Fancier's Choice in 2010. Feeding trials were 7 consecutive weeks (27 June to 15 August) in 2009 and 20 consecutive weeks (3 April to 22 August) in 2010 (Table 2). Similar to band-tailed pigeons, rock pigeons were weighed midday at the beginning and end of the feeding trial in 2009, and I measured mineral solution consumption weekly during the 2009 trial. I recorded nesting activities daily to evaluate fecundity and reproductive success during trials in 2009 and 2010. Similar to band-tailed pigeons, after the 2009 trial, treatment groups were reduced to sodium chloride solution at 3,500 ppm sodium concentration or tap water (control), and all pairs were provided unlimited access to commercially available flint grit (insoluble Cherrystone Grit made from crushed 100% quartzite rock, small No. 1, similar in size to that found in necropsied birds) and oyster shell (calcium) grit.

Reproductive performance attributes recorded for each pair and trial included 6 parameters: total number of clutches, total eggs produced, total eggs hatched, total young fledged (reaching 20 days of age), mean incubation period, and mean weight of fledglings at 20 days of age. From these parameters, I derived for each feeding pair and trial 3 more reproductive parameters including means for eggs per clutch, egg hatching rate, and young fledging rate. Hatchlings were removed from feeding trial cages at 20 days of age, the approximate fledging age for band-tailed pigeons and rock pigeons.

Statistical analyses

I calculated the change in pigeon mass for each subtrial (trial for rock pigeons) by subtracting the mass at the end of each subtrial from the mass at the beginning of each subtrial for each pigeon. Weekly fluid consumption was calculated as the mean of the weekly subsamples for each subtrial and cage.

I used generalized linear models with Type III sums of squares and Fisher's protected LSD tests (Zar 1996) to test for differences in mass and fluid consumption during feeding trials each year. I included subtrial, sex, treatment, and interaction effects, and then eliminated the cross effects in a reduced model with only main effects if interaction effects were insignificant ($P > 0.05$). Models were year specific because pairs, food items, treatment groups, and sample size differed between years. For rock pigeons, I used a nonparametric Mann-Whitney U test to evaluate differences in means for reproductive parameters among supplemental treatment groups within each feeding trial. I used SAS (SAS Institute, Inc., Cary, NC, USA) for all statistical analyses and considered test results significant if $P \leq 0.05$. Values are reported as mean ± SE.

RESULTS

Band-tailed pigeons

None of the band-tailed pigeons perished during the study and none of the pairs nested successfully during the study. Nesting behaviors were observed including some pairs copulating each year and 7 eggs produced by 5 pairs during the feeding trial in 2009 and 14 eggs produced by 8 pairs during the feeding trial in 2010.

In feeding trials involving berry food items in 2009 and 2010, change in band-tailed pigeon mass did not differ by supplemental mineral group (2009, $F_{3,184} = 1.5$, $P = 0.209$; 2010, $F_{1,91} = 0.2$, $P = 0.695$) or sex (2009, $F_{1,184} < 0.1$, $P = 0.870$; 2010, $F_{1,91} = 2.7$, $P = 0.106$), but did differ among subtrials (food items) in both years (2009, $F_{3,184} = 11.2$, $P < 0.001$; 2010, $F_{2,91} = 16.4$, $P < 0.001$). In 2009, pigeons lost mass during the first feeding subtrial (cracked corn = −8.5 ± 1.8 g) and gained mass in the subsequent 3 subtrials (red elderberry = 6.1 ± 2.2, cascara = 6.3 ± 2.8, and red elderberry = 11.3 ± 3.2 g, respectively), which did not differ. In 2010, pigeons lost mass during the first 2 feeding subtrials (Fancier's Choice = −12.5 ± 3.4 and red elderberry = −3.4 ± 2.4 g, respectively), which did not differ, but gained mass in the last subtrial (cascara = 15.2 ± 2.9 g). The mean change in pigeon mass when provided berry food items was 23.8 ± 3.4 g in 2009 and 11.8 ± 4.2 g in 2010, whereas the change in mass when provided grain was negative in both years (estimates provided above). In the feeding trial involving only Fancier's Choice in 2010, change in band-tailed pigeon mass did not differ by supplemental mineral group ($F_{1,21} = 0.6$, $P = 0.465$) or sex ($F_{1,21} = 2.3$, $P = 0.143$), and pigeons lost an average of 16.7 ± 5.6 g during the trial (25 weeks). There was some evidence consistent across and within feeding trials in that pigeons with access to supplemental sodium had apparent greater mass than those without access to sodium on average (mean change in mass: 2009 trials involving berries, 25.6 ± 4.6 g with sodium and 5.1 ± 4.9 without sodium, $n = 12$ each; 2010 trials involving berries, 4.1 ± 8.3 g with sodium and 3.0 ± 6.8 without sodium, $n = 6$ each; 2010 trial involving grain only, −12.6 ± 10.3 g with sodium and −20.9 ± 5.0 without sodium, $n = 6$ each).

Band-tailed pigeon pairs differed in total fluid consumption among treatment groups ($F_{3,89} = 3.6$, $P = 0.017$) and feeding subtrials ($F_{3,89} = 48.4$, $P < 0.001$) in 2009. Band-tailed pigeon pairs consumed more total fluids per week, on average, during feeding subtrials when fed cracked corn (292 ± 21 ml) than when fed berries (75 ± 9 ml). Pigeons consumed more total fluids per week across feeding subtrials in the sodium-calcium treatment group (171 ± 36 ml) than in the calcium (118 ± 18 ml) and water (101 ± 18 ml) groups, which did not differ, but the sodium group (127 ± 25 ml) did not differ from the other treatment groups. Mineral solution represented about half (calcium = 42.5%, sodium = 47.7%, and sodium-calcium = 55.6%) of the total (including tap water) fluids (calcium = 118 ± 18, sodium = 127 ± 25, sodium-calcium = 171 ± 36, and water = 101 ± 18 ml) consumed each week by pigeon

pairs. Consequently, band-tailed pigeon pairs also differed in consumption of mineral solution among feeding subtrials ($F_{3,66} = 5.49$, $P = 0.002$) in 2009, but not among treatment groups ($F_{2,66} = 2.19$, $P = 0.120$). Pigeons consumed more mineral solution per week, on average, when fed cracked corn (133 ± 26 ml) than when fed berries (47 ± 9 ml), which did not differ between red elderberry and cascara. Mineral solution consumption did not differ among feeding subtrials in 2010 ($F_{2,21} = 0.2$, $P = 0.864$), and the mean consumption per pair and week for birds with access to sodium was 59 ± 15 ml. Similarly, during the feeding trial involving Fancier's Choice in 2010, the mean consumption per pair and week for birds with access to sodium was 68 ± 26 ml.

Rock pigeons

Change in rock pigeon mass differed by supplemental mineral groups ($F_{3,51} = 12.6$, $P < 0.001$) but not by sex ($F_{1,51} = 0.6$, $P = 0.448$) during the feeding trial in 2009. Mean change in mass was least for the water treatment group (−8.5 ± 6.2) moderate for the calcium group (−30.3 ± 8.1), and greatest for the sodium (−53.5 ± 7.3) and sodium-calcium (−66.5 ± 7.8) groups, but sodium and sodium-calcium groups did not differ from each other. The primary differences were related to access to sodium, and after combining treatment groups accordingly, the mean change in mass was least ($F_{1,53} = 29.9$, $P < 0.001$) for the control group (−18.6 ± 5.3) compared to the sodium group (−60.5 ± 5.4).

Rock pigeon pairs did not differ in total fluid consumption by supplemental mineral group ($F_{3,26} = 2.1$, $P = 0.124$) during the feeding trial in 2009. Rock pigeon pairs also did not differ in consumption of mineral solution ($F_{2,38} = 3.1$, $P = 0.057$) during the feeding trial in 2009. Mineral solution represented about 20% (calcium = 21.9%, sodium = 20.4%, and sodium-calcium = 16.7%) of the total (including tap water) fluids, on average, consumed each week by pairs. Total fluid consumption by treatment group was calcium = 627 ± 46, sodium = 623 ± 49, sodium-calcium = 696 ± 41, and water = 491 ± 88 ml).

Rock pigeons were reproductively prolific during feeding trials, especially during 2010 when they had a more adequate diet (Fancier's Choice vs. cracked corn in 2009). In 2009, 30 pairs of rock pigeons initiated 25 clutches and fledged 24 young in 50 days. Each pair had no more than a single clutch. In 2010, 30 pairs of rock pigeons initiated 73 clutches and fledged 126 young in 142 days. Six pairs had 4 clutches, all in the access to supplemental sodium treatment group, and 4 pairs (2 in each treatment group) had no clutches.

There was an apparent difference in productivity between mineral treatment groups on a sum trial basis. In both feeding trials (2009 and 2010), 15 pairs of rock pigeons with access to supplemental sodium initiated more nests than those 15 pairs of pigeons without access to supplemental sodium (11 vs. 14 in 2009 and 31 vs. 42 in 2010; 27% and 35% increase in nest initiation rate associated with access to sodium, respectively). Pigeons with access to sodium also fledged more young than those pigeons without access to supplemental sodium (3 vs. 21 in 2009 and 54 vs. 72 in 2010; 600% and 33% increase in fledging rate associated with access to sodium, respectively). Because primary differences in rock pigeon change in mass and apparent differences in reproductive performance were related to access to sodium, and the elimination of calcium and sodium-calcium treatment groups in the 2010 feeding trial ($n = 15$ pairs each treatment group), I focused subsequent assessment of reproductive performance only on access to supplemental sodium (sodium vs. control mineral treatment groups).

The increased reproductive performance (young fledged) on a per pair basis for pigeons with access to supplemental sodium was statistically significant in both 2009 and 2010 (Table 4). The increased production was mostly associated with the increased number of clutches (and associated eggs and hatchlings). The mean difference in number of clutches per pair was 0.20 ± 0.14 (95% CI = −0.08–0.48) in 2009 and 0.73 ± 0.45 (95% CI = −0.20–1.66) in 2010. The number of eggs per clutch, incubation period, hatching rate, and fledging rate did not differ among treatment groups in both years, except that fledging rate differed in 2009 (Table 4) when pigeons were provided a nutritionally limited diet (cracked corn). The fledging rate was lower (0.60 ± 0.10, 95% CI = 0.38–0.82) for pigeons without access to supplemental sodium than for those with access to sodium in 2009. In

TABLE 4 Rock pigeon (*Columba livia*) reproductive performance with and without access to supplemental sodium (Na = sodium chloride at 3,500 ppm sodium concentration) provided to pigeons during feeding trials in Battle Ground, WA, USA, 2009 (50 days) and 2010 (142 days).

	None		Na			Test statistics	
Trial/parameter	Mean	SE	Mean	SE	*n1, n2*	*Z*[a]	*P*
2009							
Clutches	0.73	0.12	0.93	0.07	15, 15	1.41	0.158
Eggs	1.40	0.24	1.87	0.13	15, 15	1.73	0.084
Incubation days	17.30	0.45	16.50	0.39	10, 14	1.24	0.214
Hatched	1.73	0.19	2.00	0.00	11, 14	1.57	0.116
Fledged	0.30	0.15	1.50	0.14	10, 14	3.68	0.002
Fledging mass (g)	180.94	14.27	186.85	10.34	3, 13	0.00	1.000
Eggs per clutch	1.91	0.09	2.00	0.00	11, 14	1.05	0.295
Hatching rate	0.95	0.05	1.00	0.00	10, 14	1.10	0.272
Fledging rate	0.15	0.08	0.75	0.07	10, 14	3.68	<0.001
2010							
Clutches	2.07	0.27	2.80	0.37	15, 15	2.04	0.041
Eggs	4.13	0.53	5.53	0.72	15, 15	2.04	0.041
Incubation days	18.27	0.32	18.13	0.16	13, 13	0.34	0.738
Hatched	4.46	0.33	5.92	0.50	13, 13	2.31	0.021
Fledged	4.15	0.39	5.54	0.51	13, 13	1.98	0.047
Fledging mass (g)	300.72	5.72	336.26	5.41	13, 13	3.33	0.009
Eggs per clutch	2.00	0.00	1.98	0.02	13, 13	0.92	0.356
Hatching rate	0.94	0.03	0.93	0.03	13, 13	0.03	0.488
Fledging rate	0.93	0.05	0.93	0.03	13, 13	0.92	0.358

[a]Two-sided probability Z score.

addition to the difference in productivity, the mean difference in fledgling mass was greater for pigeons with access to supplemental sodium (35.5 ± 7.9 g, 95% CI = 19.3–51.8) at fledging in 2010, but the difference was not statistically significant in 2009 (5.9 ± 22.9, 95% CI = −43.2–55.0). Nesting cycles were frequently compressed in 2010 by pairs initiating clutches while caring for young prior to fledging. The first nest was initiated 7 days after pairing in breeding cages. Most (65%, 17 of 26) pairs initiated nests 19–24 days post pairing.

DISCUSSION

Band-tailed pigeons

Data indicate that red elderberry and cascara berries are high energy food sources for band-tailed pigeons, and that pigeons can thrive on these berries without access to supplemental sodium and calcium. Pigeons lost mass when on a grain diet in all 3 feeding trials conducted in 2009 and 2010. Pigeons maintained or gained mass in captivity on an

exclusive berry diet of elderberry and cascara berries for 85 consecutive days in summer 2009 and 64 consecutive days in summer 2010 without access to supplemental minerals. Also, pigeons survived for 2 years in captivity on a low sodium and high potassium diet of berries and grain similar to the wild berry food items pigeons consume during summer (Sanders and Braun 2022). Pigeons will consume supplemental sodium and calcium if available, but my data did not indicate that pigeon mass was significantly different for pigeons with access to supplemental minerals. The lack of statistically significant results may be related to small sample size and high variance in mass within trials influenced by timing of food and fluid consumption prior to weighing. However, there was some evidence consistent across and within feeding trials in that pigeons with access to supplemental sodium had apparent greater mass than those without access to sodium on average. Pigeons consumed little free water (about 38 ml per pigeon per week) when consuming berries with high moisture content (24–29% dry matter) and consumed considerably more free water (about 146 ml per pigeon per week) when consuming grain with low moisture content (86–90% dry matter).

Band-tailed pigeons are well suited to survive on a berry diet low in sodium and high in potassium regardless of access to supplemental sodium and calcium. In an 18-day preliminary feeding trial, rock pigeons provided cracked corn with verified enhanced 3% potassium concentration similar to that of red elderberry and cascara berries experienced a mean change in mass of −68.3 ± 3.3 g and −72.9 ± 4.7 g for birds with and without access to sodium (n = 30 pigeons in each group), respectively, and all 21 nests initiated by 30 pairs failed (T. A. Sanders, U.S. Fish and Wildlife Service, unpublished data). The feeding trial was aborted and no pigeons perished. These data suggest that supplemental potassium is not beneficial and may be harmful to pigeons, and that access to supplemental sodium may be beneficial when consuming food items high in potassium in regard to maintaining mass and improved reproductive performance.

Some birds have mechanisms that allow low-electrolyte diets. Red crossbills (*Loxia curvirostra*), and mourning doves (*Zenaida macroura*), both granivorous species, are known to have an efficient mechanism for conserving sodium ions, making supplemental salt unnecessary for sodium balance and good health even when kept on a seed diet very low in sodium (Bartholomew and MacMillan 1960, Dawson et al. 1965, Hayslette and Mirarchi 2002). Avian frugivores are known to have physiological challenges from the high moisture content, imbalance of sodium to potassium, and a diverse array of secondary metabolites in fruit pulp but may have developed physiological adaptations that allow use of this high energy food resource (Johnson et al. 1985, Levey and Martinez del Rio 2001). Levey and Martinez del Rio (2001) indicated the morphology of hummingbird kidneys appears well suited to recover electrolytes with high influx of water (Beuchat et al. 1999); some nectars have very low levels of electrolytes and abundant potassium, but little sodium (Calder and Hiebert 1983). These authors predicted that avian frugivores that feed on juicy and watery fruit will show renal traits similar to those exhibited by nectar-feeding birds (i.e., kidneys with reduced concentrating medullary tissue and increased ability to recover electrolytes). Band-tailed pigeons may have a mechanism for conserving sodium ions that allows use of berry food items low in sodium, high in potassium, and high in moisture concentrations.

My data are particularly interesting because they confirm that band-tailed pigeons can maintain mass and apparent health while consuming a diet with high potassium and low sodium without access to supplemental (i.e., nonessential) minerals. However, data suggested that access to supplemental sodium could offer band-tailed pigeons advantages in body weight maintenance or gain and potential energy to invest in reproduction when consuming a diet low in sodium and high in potassium and this could have benefits in survival probabilities. At least some band-tailed pigeons do have a strong affinity for supplemental mineral sites, returning to use them on average about once every 12 days (Sanders and Koch 2018) throughout the spring to early fall and despite hunting pressure at these sites (Jarvis and Passmore 1992). Observations of band-tailed pigeons at mineral sites indicate use of supplemental sodium is an important resource (Jarvis and Passmore 1992, Sanders and Koch 2018) if available during the breeding season. Because band-tailed pigeons did not nest in this study, it remains unknown if there are benefits to reproductive performance from access to supplemental minerals, but this seems probable based on my results on adult maintenance and weight gain. Band-tailed pigeons are highly nomadic (Jarvis and Passmore 1992, Keppie and Braun 2000), and a pigeon's use of supplemental mineral depends on juxtaposition of supplemental mineral sites to an abundant and dependable food source (Sanders and Jarvis 2003), composition of the diet (Sanders and Braun 2022), breeding status (Sanders and Jarvis 2000), and the availability of predictable and dependable supplemental mineral sites within and among years (Sanders and Koch 2018).

Rock pigeons

Like band-tailed pigeons, rock pigeons lost mass during a 50-day feeding trial where pigeons were fed a nutritionally limited diet of cracked corn. But unlike band-tailed pigeons, there was a greater negative change in mass for pigeons that consumed supplemental sodium than for those that did not. Despite the loss in mass associated with sodium solution consumption, pigeons that consumed supplemental sodium had greater reproductive performance. Pigeons lost mass with use of supplemental sodium possibly because the sodium allowed greater investment and success in reproduction. During the trial in which I measured mass, the primary reproductive difference between treatment groups was fledging rate. There was also an increase in the number of clutches for the pigeons with access to supplemental sodium, but this would seem to impact female mass, a pattern we did not observe. Migratory birds are known to face reproductive costs in maintenance and other life-history aspects when time or energy is invested in reproduction representing a prominent life-history tradeoff observed in nature (Williams 1966, Stearns 1989, Mitchell et al. 2012).

Pigeons with access to sodium fledged more young than those pigeons without access to supplemental sodium. The increased production for pigeons with access to supplemental sodium was primarily associated with the increased number of clutches. However, in 2009, when pigeons were fed a nutritionally limited diet of cracked corn, the fledging rate was lower for pigeons without access to supplemental sodium than for those with access to sodium. In addition to the difference in productivity, and fledging rate, fledgling mass was greater for pigeons with access to supplemental sodium at fledging in 2010, but the difference was not statistically significant in 2009, possibly because of the nutritionally limited diet. The feeding trial data provide strong evidence that use of supplemental sodium by rock pigeons results in increased fecundity and can result in increased fledgling survival and greater mass of young at fledging. The greater mass at fledging could result in increased first-year survival rate for these birds compared to fledglings with lesser mass. This is an interesting finding for a columbid species that is not known to use supplemental sodium sites. My results are consistent with the findings of Vieira et al. (2003) that show increased body weight gain and feed conversion in broiler chicks in the first week post-hatching with dietary sodium between 0.38 and 0.40%; however, responses to increased dietary sodium did not remain with broilers at 6 weeks of age.

These results on reproductive performance from rock pigeon feeding trials may be applicable to band-tailed pigeons. Considering the especially low sodium and high potassium natural diet of band-tailed pigeons, access to supplemental sodium could offer advantages in fecundity and hatchling survival rates through increased efficiency in food conversion and hatchling body weight gain, particularly when feeding on a diet with high potassium and moisture content and low sodium content. The band-tailed pigeon's behavior in use of supplemental mineral sites could have developed over time because of benefits in maintenance or gain in adult body weight and reproductive performance from access to supplemental sodium. This behavior could be most prominent among some Pacific Coast band-tailed pigeons because of the number of natural mineral sites known to occur throughout the species range, particularly during the breeding season in the Pacific Northwest. Band-tailed pigeons congregate at and use supplemental sodium sites when they are available (Sanders and Jarvis 2000, Sanders and Jarvis 2003, Sanders and Koch 2018, Sanders and Braun 2022). However, band-tailed pigeons may survive and reproduce (Sanders and Braun 2022) without access to supplemental mineral sites when consuming berry diets with low sodium and high potassium.

MANAGEMENT IMPLICATIONS

Band-tailed pigeons consuming a berry diet with low sodium and high potassium can survive and maintain body mass without access to supplemental sodium (and calcium), but it remains unknown if access to supplemental sodium (and calcium) is associated with increased reproductive performance or recruitment. Rock pigeons have increased reproductive performance with access to supplemental sodium, having fledged ≥33% more young and at a higher body mass with access to supplemental sodium. This could have advantages in hatching year survival

(i.e., recruitment). The band-tailed pigeons' use of supplemental mineral sites could offer advantages in fecundity and hatchling food conversion and body weight gain as young transition from crop milk to food items, particularly berries. The benefit to band-tailed pigeons' fitness from use of supplemental sodium during the breeding season seems likely but remains unverified and should be evaluated via a feeding trial experiment where these birds have previously demonstrated propensity to breed in captivity. This is imperative to determine the necessity and benefits of creating or protecting supplemental mineral sites for monitoring, managing, and conserving this species. Natural mineral sites used by band-tailed pigeons should be conserved until additional information is available for evaluation. Comparison of counts of band-tailed pigeons at mineral sites must be interpreted cautiously until the factors that influence the band-tailed pigeon's use of mineral sites in space and time can be determined.

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CONFLICTS OF INTEREST

The author declares no conflicts of interest.

ETHICS STATEMENT

This research was conducted in compliance with the Guidelines for the Use of Wild Birds in Research (Fair et al. 2010).

DATA AVAILABILITY STATEMENT

Data available on request due to privacy or ethical considerations.

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