Long-term consistency of dispersal between two colonies of northern elephant seals

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Abstract

Dispersal allows the extinction-recolonization dynamics of metapopulations and is crucial to recolonization of former range in endangered species. Yet few studies quantify dispersal and even fewer examine consistency of dispersal over many years. The northern elephant seal (*Mirounga angustirostris*) provides an example of the importance of dispersal. It quickly recolonized its former range after near extirpation by 19th century hunting, and dispersal events restablishing its colonies were observed, but the rate of dispersal was never quantified. Here we provide 17 years of dispersal rates based on resightings of > 1000 permanently marked individuals observed from birth to breeding at two colonies 200 km apart in California. An average of 16.7% of the females born at the Piedras Blancas colony dispersed northward to breed at Año Nuevo, while 7.3% of those born at Año Nuevo dispersed southward to Piedras Blancas. There were no temporal trends in these rates. During the study, the population at Piedras Blancas expanded 15-fold, while Año Nuevo abundance was stable. In the early years of the study, far more dispersal was directed away from the small colony toward the large,

rejecting a prediction of density-driven dispersal. Consistently high natal dispersal in northern elephant seals means the population should be considered a single large unit in terms of response to environmental change. High dispersal was fortuitous to the past recovery of the species, and continued dispersal means elephant seals will likely continue to expand their range and colonize new breeding sites.

Introduction

Dispersal and immigration are vital statistics of populations. Besides effecting gene flow and evolution, dispersal regulates metapopulation dynamics, and by overcoming local extinctions it can be crucial in species recovery from population crashes (Chilvers & Wilkinson, 2008; Mestre *et al.*, 2021; Winkler *et al.*, 2005). The northern elephant seal offers a clear example, because following near extermination by 19th-century hunters, it readily dispersed to reoccupy its former range (Bartholomew & Hubbs, 1952; Lowry *et al.*, 2014; Townsend, 1912). During 50 years of research in California, we observed dispersal and documented new colonies formed by immigrants (Le Boeuf *et al.*, 2011), but quantifying dispersal has been difficult, as is often the case in large animals that move long distances (McCaslin *et al.*, 2020; Tittler *et al.*, 2009). Without precise estimates of rates of movement, we do not know whether dispersal continues now that the range is reestablished, and we cannot compare the importance of dispersal in elephant seals to other species (Bowne & Bowers, 2004; Chilvers & Dobbins, 2021). Here we fill the gap by quantifying dispersal rate in two directions in 17 consecutive birth cohorts. In a review of emmigration rates, only four studies included more than 17 years (Matthysen, 2005).

Seals and other colonial animals have an important advantage in measurements of dispersal because breeding locations are discrete, so dispersal is a binomial process, either happening or not, and there are limited locations that must be searched to identify migrants. These features contrast with many terrestrial birds that have been the subject of dispersal work, where every individual disperses some distance (Greenwood & Harvey, 1982; McCaslin *et al.*, 2020; Winkler *et al.*, 2005). We have been applying lifetime marks to female elephant seals for 30 years at two major colonies in central California, Año Nuevo and Piedras Blancas, and recording sightings of those animals at both colonies

every year, so we can now be precise about dispersal in both directions. What percent of females born at one colony moved to the other to breed? Is there a asymmetry in direction, so females move more often northward or southward? We also test predictions of density-driven dispersal, since the Piedras Blancas colony was small at the outset but expanded greatly during our observations. Since Año Nuevo was large throughout, we test whether dispersal was greater from the large colony to the small in the early years, and whether that changed through time.

Materials and Methods

Ethics statement

Seal observations were authorized under Marine Mammal Research Permits 347, 404, 486-1506, 486-1790, 684, 704, 705, 774-1437, 774-1714, 836, and 14097; National Marine Sanctuary Permits GFNMS/MBNMS/ CINMS-04-98, MULTI-2002-003, MULTI-2003-003, and MULTI-2008-003; and Marine Mammal Protection Act Permit 486. Access to park land was granted by the California Department of Parks and Recreation.

Study sites and colonies

Our study sites are the largest northern elephant seal colonies on the mainland, providing accessibility and large samples (other large colonies are on islands). Point Piedras Blancas is at 35.7° N and Año Nuevo at 37.1° N latitude in California. At both sites, female elephant seals gather in large groups on flat sand beaches and give birth to a single pup per year from December-February. Pups are weaned an average of 25 days after birth when mothers depart to forage, and weanlings are easily approached and tagged on the beach before they go to sea (Le Boeuf *et al.*, 1972). The Año Nuevo colony has had pups every winter since 1961, and the Piedras Blancas colony since 1991, and both have had > 1000 pups born each year since 1997 (Le Boeuf *et al.*, 1972; Lowry *et al.*, 2014).

Tagging and lifetime breeding records

Plastic cattle tags were inserted in the interdigital webbing of the hind flippers of weanlings (Le Boeuf *et al.*, 1972). Since 1998, most tags deployed at both sites were Jumbo Roto tags. We consistently searched both colonies during the winter breeding season, when females with their pups hold their ground and allow observers closely. Tags were generally read with binoculars from 3-5 m away from animals at Año Nuevo, and with telescopes from bluffs 5-10 m away at Piedras Blancas. For this study we focus on pups tagged during 1994-2010. Because females start breeding at age 3-4 (Le Boeuf *et al.*, 2019; Reiter & Le Boeuf, 1991), observations from 1997-2018 provide multiple opportunities to observe those cohorts during their breeding lifetimes. We assumed any female age 3 or older observed during the breeding season was breeding because 97.5% of adult females in the colony give birth (Le Boeuf *et al.*, 2019; Le Boeuf & Reiter, 1988).

Dispersal rate

Our focus is natal dispersal of females, defined as movement from the birth colony to a different colony on the first breeding attempt. The natal dispersal rate is the probability that a female that is alive at its first breeding attempt is at a colony different from its birth place. Animals that die prior to breeding do not figure in this rate. We record natal dispersal based only on the location of an animal's first breeding observation; later breeding attempts were not relevant. Adult dispersal is the probability that an animal moves between colonies after breeding, and we estimate that separately.

To estimate natal dispersal, define T_i as the total number of females tagged at colony i, and B_i the number of those observed breeding at any time in the future. Now consider b_{ij} as the subset of B_i first observed breeding at colony j. In this study, $i, j \in (1, 2)$, and $B_1 = b_{11} + b_{12}$, $B_2 = b_{21} + b_{22}$. The ratio $\mu_{ij} = b_{ij}/B_i$ is a measure of natal dispersal rate from colony i to colony j. Any of the original T_i females never seen breeding do not enter into the calculation, since we know nothing about their fate; they may have dispersed then died before a breeding observation, or simply died before breeding.

Detection of adult females

A concern with the calculation of natal dispersal is the failure to detect females that are present and breeding. Define detection, δ, as the probability that a tagged female on a colony in one winter season is observed. At Año Nuevo, we know that females are not always detected, and estimated annual detection $\delta = 0.6$ from a mark recapture analysis (Condit *et al.*, 2014). The concern here is that a difference in detection between the two colonies will introduce a bias in dispersal estimates. Since we are calculating dispersal based on lifetime observations, the relevant bias would be a difference in lifetime detection.

A simple example illustrates. Consider one cohort from colony 1 that ended up with 100 females breeding over their lifetimes, 90 resident where they were born and 10 emigrating to a second colony, and a parallel cohort at colony 2 with 90 breeding as residents and 10 emigrating to colony 1. Both colonies had 10% dispersal. What if only half the females were detected over a lifetime at colony 1, while 80% were detected at colony 2? Then the number of breeders born at site 2 and resident at site 2 would be estimated as $b_{22} = 90 \times 0.8 = 72$, and the number emigrating estimated as $b_{21} = 10 \times 0.5 = 5$, leading to an estimated dispersal from colony 2 to 1 of $\mu_{21} = b_{21}/B_2 = 5/(5 + 72) = 0.065$. The opposite calculation leads to $\mu_{12} = b_{12}/B_1 = 8/(8 + 45) = 0.15$. Dispersal toward the colony with fewer observations will be underestimated and dispersal toward the well-observed colony overestimated.

We will correct for this bias using the observations of tagged females because they allow estimates of lifetime detection at both colonies. Two other probabilities are required for the calculation: annual survival of breeding females, σ, and annual retention of tags, ρ (the opposite of the loss of all tags). There are previous estimates of survival and tag loss (Condit *et al.*, 2014; Le Boeuf & Reiter, 1988), however, we demonstrate that they are not needed separately. Survival and retention probabilities only appear in calculations as a product, and that product can be estimated from observations of tagged cohorts presented here (Appendix S1).

Define the product of survival and tag retention as $\Phi = \sigma\rho$. This is the probability that a female survives and retains her tag, so we call it the rate of return – the probability that a marked animal returns with the mark. Next, define a rate of reappearance, Ψ,

as Φ multiplied by annual detection, δ. Reappearance is the probability that a female survives, retains her tags, and is detected. Both return Φ and reappearance Ψ can be derived directly from observations: Φ can be estimated as the probability that an individual observed in one year is seen again the next year, since that requires survival, tag retention, and detection; and Ψ can be estimated from the age distribution of tagged females throughout the observation period. Appendices S1 and S2 give detailed derivations. Return rate and reappearance rate differ precisely by detection probability, ie annual detection $\delta = \Psi/\Phi$. This allows us to estimate detection separately for the two colonies; neither survival nor tag retention is needed, only their product.

But we need lifetime detection, Δ, the probability that a female breeding at a colony is observed at least once there, not annual detection. We derive in Appendix S3 the following relation:

$$\Delta = \frac{\delta}{1 - \Phi + \delta\Phi}, \tag{1}$$

giving Δ as a function of three quantities known separately at each colony. The number of tagged females observed over a lifetime breeding at one colony can then be corrected for detection, with $b = N/\Delta$, where N is the observed number and b the corrected total.

Adult dispersal

Lifetime detection would be complicated if breeding females move from one colony to another during their adult lifetimes, which is adult dispersal. If females move often as adults, estimates of natal dispersal will be confounded by adult dispersal in cases where females are not observed in their first breeding year. To check this possible error, we separately estimated adult dispersal rate as a simple calculation from observations of marked females. We found every case where a female was observed in consecutive breeding seasons and tallied the fraction of those that were at each of the two colonies. The proportion at a different colony in the second year is a direct estimate of annual adult dispersal.

Error propagation

Credible intervals on the number dispersing were calculated using the beta-distribution to describe the posterior sampling distribution, b_{ij} out of the total B_i (Press & Press, 1989), since the b_{ij} are binomially distributed. Additional sources of error arise in the calculation of lifetime detection, which depends on rates of return and reappearance. It was thus necessary to propagate error from each step to the final estimate.

First, the adult reappearance rate, Ψ, was calculated as a ratio of integers, and we again used the beta-distribution as an estimate of the posterior distribution of Ψ. The 95% credible intervals were assumed to represent four standard deviations, assuming a Gaussian distribution, which is a good approximation to the binomial given large sample size. The standard deviation (σ) of the observed count (individuals reappearing) was thus estimated as one-quarter the width of the 95 percentiles from the beta posterior, and this was divided by the mean μ to yield the coefficient of variation, $CV_\Psi = \sigma/\mu$, for the rate Ψ.

The next term needed in the calculation is the rate of return Φ, estimated from a standard linear regression and the resulting slope and standard error (Appendix 2); the ratio of the standard error to the slope was used as the coefficient of variation, CV_Φ. The CV for lifetime detection was then calculated from the CVs of reappearance and return rates, since it depends ultimately on those two parameters (Eq. 1). CVs are propagated by summing squares (Meyer, 1975),

$$CV_\Delta^2 = CV_\Phi^2 + CV_\Psi^2. \tag{2}$$

Modeling emigration rates

In order to incorporate all sources of error in estimates of dispersal rates, we used a Bayesian method to fit parameters. This allowed error in the detection probability, Δ, to be included as a prior distribution. The prior at a colony had a mean Δ equal to the single best estimate across all years (Eq. 1), and a standard deviation based on the coefficient of variation (Eq. 2), $SD_\Delta = \Delta \times CV_\Delta$. The observations were the number of females from each cohort, at each colony, that emigrated to the other colony (b_{ij}) and the number that remained as residents (b_{ii}). The Bayesian method produced estimates

of the emigration rate, μ_{ct}, using subscripts c for colony and t for cohort, and mean rates, $\widehat{\mu_c}$, for each colony, along with posterior distributions of each. The rate μ_{ct} was log-transformed so a Gaussian error could be used in the parameter-fitting; results are presented after back-transforming. The parameter fitting is based on likelihood of the observed number of females as a function of emigration and detection parameters.

Variation in dispersal with colony size

The Piedras Blancas colony grew by 15-fold over the course of the study, from 293 breeding females in 1994 to 4469 in 2010 (Lowry *et al.*, 2014). In early years, breeding females would have found relatively unoccupied beaches, in contrast to later years, when arriving animals found many beaches occupied. We do not know, however, whether colony density (females per beach area) increased with colony size, because animals spread out as the colony expanded. In contrast, the Año Nuevo colony was relatively stable, varying by no more than 22% over the same period (maximum 2731 females in 1995, minimum 2144 in 2010 (Le Boeuf *et al.*, 2011)), and seals occupied the same beaches throughout. We tested whether dispersal rate varied through time with a linear regression between annual rate of emigration (μ_{ct}) and year. We also compared rates from Año Nuevo toward Piedras Blancas and vice versa to test the prediction that emigration was more frequent from high density to low density colony.

Results

Observed natal dispersal

Observed juvenile emigration events were more frequent from Piedras Blancas to Año Nuevo than vice versa (Table 1). Combining all 17 cohorts, there were 468 pups tagged at Piedras Blancas that were observed as breeding adults: 344 at their birth colony and 124 that emigrated to Año Nuevo (26.5% emigrated). There were 601 pups from Año Nuevo that were observed breeding: 566 as residents and 35 as emigrants to Piedras Blancas (5.8% emigrated). But this comparison is biased by detection, and the correction requires estimates of lifetime detection.

Rate of reappearance of tagged females

At Piedras Blancas, the 468 breeding females had 669 breeding records over all years of the study, and 110 were observed in the year following (Table 2). The reappearance rate was $\Psi = 110/669 = 0.164$. The coefficient of variation was 0.085. Two of the 669 seen in consecutive years were emigrants to Año Nuevo in the second year, so adult dispersal $= 2/669 = 0.003$.

At Año Nuevo, the 601 observed breeders had a total of 2289 breeding records over all years. Of those, 1293 were observed breeding in the following year (Table 2), so the rate of reappearance was $\Psi = 1293/2289 = 0.565$, much higher than at Piedras Blancas. The coefficient of variation was 0.0180. Eight of the 2289 females moved to Piedras Blancas in the second year, so adult dispersal $8/2289 = 0.003$.

Rate of return of tagged females

The rate of decay of observed females per additional year of age was -0.224 ± 0.0070 at Año Nuevo and -0.244 ± 0.0196 at Piedras Blancas (Fig. S1). These lead to estimates of the rate of return for females, $\Phi = 0.799$ at Año Nuevo and $\Phi = 0.783$ at Piedras Blancas (coefficients of variation 0.031 and 0.080). The rates were statistically indistinguishable (confidence interval for Año Nuevo, 0.79-0.81; for Piedras Blancas, 0.75-0.81).

Annual detection of breeding females

The annual detection probability, $\delta = \Psi/\Phi = 0.565/0.799 = 0.707$ at Año Nuevo. This was more than three-times higher than at Piedras Blancas, where $\delta = 0.164/0.783 = 0.209$.

Lifetime detection

At Piedras Blancas,

$$\Delta = \frac{0.209}{1 - 0.783 + 0.209 \cdot 0.783} = 0.549, \tag{3}$$

and at Año Nuevo,

$$\Delta = \frac{0.707}{1 - 0.799 + 0.707 \cdot 0.799} = 0.923 \tag{4}$$

(Eq. 1). The average female spending a lifetime breeding at Piedras Blancas was thus only 60% as likely to be detected as a similar female at Año Nuevo. The coefficients of variation, propagated from errors in Φ and Ψ, were 0.036 at Año Nuevo and 0.117 at Piedras Blancas.

Corrected natal dispersal

The higher lifetime detection probability at Año Nuevo means that the observed number emigrating toward Año Nuevo (Table 1) was biased upward. The corrected rate of emigration from Piedras Blancas to Año Nuevo over all cohorts was 0.167 (credible intervals, 0.104-0.247), more than double the reverse rate from Año Nuevo to Piedras Blancas, 0.073 (0.041-0.113). The 95% credible intervals thus overlapped slightly. There was considerable year-to-year variation in the northward rate (toward Año Nuevo), indeed the rate of 0.41 for the cohort born in 2000 was significantly higher than the rate of 0.17 in 2004 (Fig. 1). There was much less variation in the southward direction, and none was significant (Fig. 1). The northward rate was higher than the southern in 15 of 17 cohorts, and significantly higher in the 1995 and 2000 cohorts (Fig. 1).

Dispersal and density

There was no temporal trend in dispersal in either direction (northward, regression with year, slope $b = -0.003, p = 0.55$; southward, $b = 0.002, p = 0.89$). During the early years of the study, when the Año Nuevo colony had far more animals than Piedras Blancas, dispersal was higher from Piedras Blancas toward Año Nuevo (Fig. 1).

Discussion

During the 1970s and 1980s, young elephant seals in California were observed emigrating from their birth colonies to establish new colonies (Allen *et al.*, 1989; Le Boeuf *et al.*, 1974), but rates of dispersal were not estimated. Our results here confirm dispersal

and add quantitative results over many years. Juvenile females dispersed between two major colonies 200 km apart at a substantial rate, 16.7% in the northward direction and 7.3% southward. These rates are higher than those published for other pinnipeds, including harbor seals (*Phoca vitulina*) and gray seals (*Halichoerus grypus*) in Europe. In harbor seals, close to 10% of breeding females emigrated to colonies within 10 km of their birthplace, but none dispersed more than 20 km (Harkonen & Harding, 2001), while in gray seals, the fraction dispersing was $< 5\%$ among all colony pairs, though that was based on population models, not direct observations (Harrison *et al.*, 2006). Interestingly, a literature review covering many species (but no marine mammals), the mean fraction dispersing was 15% (Bowne & Bowers, 2004), close to what we observed. How dispersal was measured, and observed distances, were extremely variable among species, so this is not a safe generalization.

Dispersal rates between Año Nuevo and Piedras Blancas remained consistently high over 17 consecutive cohorts, and though there were fluctuations, there was no long-term trend. During that period, the population at Piedras Blancas grew 15-fold while the number at Año Nuevo colony declined slightly. There is thus no indication in these results that emigration responded to colony size, since rates did not decline through time at Piedras Blancas. Moreover, during the mid-1990s, there was more dispersal from the smaller Piedras Blancas colony toward the larger Año Nuevo. These results do not support earlier observations that colony size drove decisions of young females to emigrate to found new colonies (Le Boeuf *et al.*, 2011). Those observations were based on the Año Nuevo Island colony, where the females are tightly packed in a few large groups, and most individuals encounter high density of near neighbors. In contrast, the Piedras Blancas colony spread to new beaches as it grew, so it is not clear whether individuals faced higher density in 2015 than they did in 1995. In a 2005 review of studies examining emmigration and population density, Matthysen (Matthysen, 2005) found a positive relation in some studies, but no relation in others. A recent, large study of falcons (*Falco sparverius*) found no correlation between population density and frequency of dispersal (McCaslin *et al.*, 2020).

There was directionality in dispersal in our results, since the northward rate was more than double the southward. The difference was at the margin of statistical significance, and it should be further tested, but the northward flow fits the elephant seal migration.

Females move northwestward from their breeding colonies in California toward distant foraging grounds (Aurioles *et al.*, 2006; Robinson *et al.*, 2012), thus animals born at Piedras Blancas passed Año Nuevo on the migration, but not vice versa. The feeding grounds are considerably further than the distance between colonies, and from that perspective dispersal distances in elephant seals are not high. A tendency for long-distance migrants to disperse well compared to non-migrants has been demonstrated in birds (Paradis *et al.*, 1998).

Our dispersal estimates include thorough analysis of error, most importantly the bias caused by unequal detection probabilities. This bias is often mentioned in studies of bird dispersal but is difficult to quantify (Winkler *et al.*, 2005). We were able to estimate lifetime detection from many years of resightings of long-lived females, and we demonstrated much higher detectability at Año Nuevo than Piedras Blancas. Better detection at Año Nuevo can be attributed to better beach access as well as student participation in the university-sponsored research. Wide credible intervals in dispersal rates arose because of thorough error propagation.

These natal dispersal rates may be underestimates because we only included two colonies, and we have evidence of movement to additional colonies. In Condit et al. (Condit *et al.*, 2014), we reported the lifetime fate of three cohorts of females branded at Año Nuevo during the 1980s, including three adjacent colonies. We found that seven emigrated of the 37 that bred (18.9%); this was before the Piedras Blancas colony existed, and the emigrants were at the Farallon and Point Reyes colonies north of Año Nuevo. In an analysis of three cohorts (Zeno *et al.*, 2021), all four colonies were included. No correction for detection was incorporated, but the observed number of emigrants from Piedras Blancas to the other two colonies was nearly as high as the number moving to Año Nuevo, while the number dispersing from Año Nuevo to the other two was even higher than the number moving to Piedras Blancas. There may be additional dispersal to the Channel Island colonies, 200 km south of Piedras Blancas, as well, but observations at those large island colonies are much more difficult. Overall, we have reason to believe that total natal dispersal rates are even higher than those reported here, perhaps reaching 20%.

Once breeding, adult females move at much lower rates. In the cohorts we studied, fewer than half a percent moved over consecutive years. Northern elephant seal colonies

are thus well-mixed genetically in that juveniles move among them at substantial rates, but most adults spend their lives at a single colony. In terms of response to the environment or prey abundance (Goetsch *et al.*, 2018), we conclude that the northern elephant seal should be treated as one large population.

Perhaps most important is the role of dispersal in recovery from population bottlenecks, and this is clear in northern elephant seals. Nearly extinct in 1892 (Townsend, 1912), the species refilled its range within 70-80 years (Lowry *et al.*, 2014; Stewart *et al.*, 1994). We demonstrated here that dispersal continues now, even after the range has filled, and elephant seals are thus poised to expand their range further, as they recently have at King Range in northern California (Goley & Levy, 2021). In other pinnipeds, poor dispersal may be a primary reason for slow recovery (Chilvers & Dobbins, 2021). The fact that elephant seals disperse well appears to be a fortuitous trait in the face of the 19th century decimation by hunters.

Supporting Information

Three Appendices provide complete derivations of the estimates of annual and lifetime detection of breeding females. One Supplemental Figure shows the rate of decay of the number of tagged females versus age at both colonies.

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Table 1. Observed dispersal in annual cohorts of female elephant seals between two colonies. Tagged gives the total number of females tagged as pups each year at the two colonies. Breeding gives the number of those observed breeding at least once over their lifetimes. Those are divided into two groups, Resident, the number first breeding where they were born, and Emigrant, first breeding at the opposite colony.

	Año Nuevo born				Piedras Blancas born			
Year	Tagged	Breeding	Resident	Emigrant	Tagged	Breeding	Resident	Emigrant
1994	240	24	24	0	120	13	11	2
1995	420	55	52	3	152	40	23	17
1996	271	51	46	5	148	41	33	8
1997	210	16	15	1	14	3	3	0
1998	211	37	36	1	155	35	23	12
1999	146	21	21	0	158	24	16	8
2000	263	46	45	1	156	32	14	18
2001	108	16	14	2	158	45	29	16
2002	139	40	39	1	158	42	36	6
2003	177	46	39	7	138	29	22	7
2004	166	25	23	2	150	31	31	0
2005	376	42	36	6	176	16	15	1
2006	282	28	28	0	132	20	15	5
2007	365	56	54	2	176	31	25	6
2008	213	26	25	1	174	22	18	4
2009	296	46	44	2	123	16	10	6
2010	208	26	25	1	196	28	20	8
Total	4091	601	566	35	2486	468	344	124

Table 2. Females observed over consecutive years.

	AN born			PB born		
Year	Observed	Reappear	Emigrated	Observed	Reappear	Emigrated
1994	92	43	0	25	5	0
1995	225	120	1	51	7	0
1996	186	110	1	76	11	0
1997	65	36	0	8	2	0
1998	191	113	0	61	18	0
1999	143	89	3	29	5	1
2000	207	96	0	24	4	0
2001	136	79	0	52	9	0
2002	158	93	2	75	13	0
2003	157	92	1	55	11	0
2004	53	24	0	62	9	0
2005	134	95	0	27	1	0
2006	101	59	0	22	3	0
2007	164	95	0	40	6	0
2008	68	36	0	24	4	1
2009	135	72	0	14	0	0
2010	74	41	0	24	2	0
Total	2289	1293	8	669	110	2

Figure 1. Juvenile dispersal. Dispersal of juveniles born at Piedras Blancas to breed at Año Nuevo is red (mean 0.175, credible intervals 0.118-0.243); dispersal from Año Nuevo to Piedras Blancas in blue (mean 0.075, CI 0.047-0.110).

Appendix S1: Annual detection

The annual probability that a breeding female elephant is detected on a colony, given that she is present, can be derived from observations of tagged females in consecutive years. It requires knowledge of survival and tag retention probabilities. Define annual detection δ, annual survival σ, and annual tag retention ρ.

Given that a female is alive in year t, the probability that she is alive and retains her tag at $t+1$ is the product $\sigma\rho$. Then the probability she is detected at $t+1$ is $\delta\sigma\rho$: the probability she is alive, retains her tags, and is detected. We call this the rate of reappearance, Ψ.

From those detected in one year, we have a simple and direct measure of Ψ. Define N_0 as the number of tagged adult females breeding in one year at one of our study colonies. The number of those detected is δN_0. A year later, $N_1 = \rho\sigma N_0 = \Psi N_0$ of those are alive and still have tags, and $\delta\Psi N_0$ of those would be detected. Thus, the ratio of those detected at year 1 and at year 0 is exactly Ψ. This calculation can be calculated at any colony, in one pair of years, or by summing across all cases where observations occurred in consecutive years.

In Appendix S2, we derive estimates for the product $\sigma\rho$ at each colony. Since

$$\delta = \Psi/(\sigma\rho), \tag{5}$$

we then have estimates of detection probability of breeding females at both colonies.

Appendix S2: Rate of return

We demonstrate here that the product of survival and tag retention, $\sigma\rho$ (Appendix S1) can be estimated easily from observations of tagged animals. The annual detection term δ is not needed in these calculations given the assumption that δ is constant at all adult ages. We call $\sigma\rho$ the rate of return, Φ, because it refers to animals that come back (with tags), in contrast to the rate of reappearance defined in Appendix S1, which is animals that come back and are observed. As for detection, we assume both $\Phi = \sigma\rho$ is constant for a female's lifetime, until she reaches the age of senescence at 17 years. Lifetime survival curves suggest that both σ and δ are constant [(Condit *et al.*, 2014)], with senescence setting in at age 17. Female behavior on the breeding colony is consistent at all ages 5 and above, also supporting a constant detection term. We do not have independent information on how tag retention, ρ, changes with age, and we return to this later.

Consider a cohort of females breeding for the first time. Call the number of animals in the cohort N_0. Then $D_0 = \delta N_0$ is the number of females observed in their first year, which we call $a = 0$. Note that a is not a year, since $a = 0$ is the first breeding year of many females, and includes many different calendar years.

For animals one year older, $a = 1$ and the number returning (alive and tagged) is $N_1 = \sigma\rho N_0 = \Phi N_0$. The number of those detected is $D_1 = \delta N_1 = \Phi N_0$. At subsequent ages,

$$\begin{aligned} D_t &= \delta N_a \\ &= \delta\Phi N_{a-1} \\ &= \delta\Phi^{a-1} N_0. \end{aligned} \tag{6}$$

The exponent is $a-1$ because we define the initial cohort as females alive and breeding

for the first time at $a = 0$, so the survival probability until year a requires $a - 1$ survival steps. Taking logarithms,

$$\ln D_t = C_0 + C_1(t - 1), \tag{7}$$

where the constants are $C_0 = \ln \delta + \ln N_0$ and $C_1 = \ln \Phi$. The number of animals alive at successively greater ages declines linearly with time, and the slope is $\ln \Phi$. We thus have a simple way of estimating that probability of reappearance, Φ. Detection δ appears in the intercept C_0 but not the slope, C_1. That comes from the assumption that δ is constant from year to year, so its impact cancels out. Every year, the number of animals observed is smaller than the number alive by the constant term δ.

Nearly all females begin breeding by age 5, and senescence sets in at age 17. We thus calculated the age distribution over ages 5-15 to estimate the rate of reappearance. The slopes at the two colonies were indistinguishable (Fig. S1), leading to an estimated probability of reappearing from year to year of $\sigma = 0.799$ at Año Nuevo and $\sigma = 0.783$ at Piedras Blancas. The slopes did not change significantly in older animals, however slopes were steeper at both colonies after age 10. We demonstrated no change in survival up to age 15, but it is possible that tag loss increases beyond age 10, though it is evidently not by much.

Appendix S3: Lifetime detection

Now we derive the probability that a breeding female elephant seal is detected at least once in her lifetime, given that she bred at least once. Again, we use the annual return rate, Φ, which is the product of annual survival σ and tag retention, rho, and annual detection, δ, and we rely on the assumption that all three are constant through a female's lifetime, until the age of senescence. We also must assume that a female's detection in one year is independent of her detection in other years, and we do not have evidence to support that assertion.

Female elephant seals can breed many years, and assuming independence from year to year, long-lived females will almost certainly be detected. Lifetime non-detection is most likely in females that breed once then die. The full derivation requires the probability of breeding once then dying, breeding twice then dying, etc.

Define lifetime detection as Δ. Since lifetime detection requires just one annual detection, it works best to use a non-detection probabilities, annual $\lambda = 1 - \delta$ and lifetime $\Lambda = 1 - \Delta$, because lifetime non-detection requires zero detections, whereas lifetime detection means 1 or 2 or 3 ... detections. The calculation begins with a group of females that are present on the breeding colony for the first time in their lives, at $a = 0$. Consider the subset of this group that returns in exactly n breeding seasons, then dies (or loses tags), so there are n chances to detect this group. Failure to detect every single season is λ^n, so the probability of lifetime non-detection over exactly n seasons is

$$\Lambda(n) = \lambda^n. \tag{8}$$

Since females have variable lifetimes, we need to calculate the probability of each lifetime n. Call $P(n)$ the probability that the average female elephant seal lives returns in n breeding seasons. Because we assume the initial cohort was already alive in the first breeding season, an additional $n - 1$ survival and tag retention events are required. This is a common Markov calculation, finding the probability of one precise sequence of events, $n - 1$ consecutive successes (alive with tags), then one last death (or tag loss). This is the only sequence of events leading to a lifetime of exactly n seasons, and its probability is

$$P(n) = \Phi^{n-1}(1-\Phi). \tag{9}$$

Φ was defined above as the annual return rate, encompassing both survival and tag retention. Equations 8 and 9 together give the probability that a female returns exactly n years yet is never detected.

We need this calculation for every lifespan: those females that return exactly 1 year, and those that return exactly 2 years, and those that return exactly 3 years, etc. Each of those groups has a number of females given by 9, and each is subdivided into two smaller groups, those not detected and those detected, the former from (Eq. 8). The product of Equations 8 and 9 in a single lifespan group gives the number of females in that group that were never detected, so summing over all those products yields the total number never detected,

$$\begin{aligned}\Lambda_{tot} &= \sum_a (1-\Phi)\sigma^{a-1}\lambda^a \\ &= \lambda(1-\Phi)\sum_a (\Phi\lambda)^{a-1}.\end{aligned} \tag{10}$$

The summation runs from $a = 1$ to $a = \infty$. The second version is rewritten so that the two terms inside the summation have the same exponent, $a - 1$. Then Equation 10 is an infinite geometric series, each term a factor Φ times the previous. In reality, the series would have to be curtailed when senescence starts, but the size of the seventeenth term is vanishingly small, so the infinite approximation is very close. The sum of an infinite geometric series is the first term, $\lambda(1-\Phi)$, divided by one minus the ratio. Since we need the total number detected, $\Delta = 1 - \Lambda$, we have

$$\begin{aligned}\Delta_{tot} &= 1 - \frac{\lambda(1-\Phi)}{1-\Phi\lambda} \\ &= \frac{1-\lambda}{1-\Phi\lambda} \\ &= \frac{\delta}{1-\Phi+\delta\Phi}.\end{aligned} \tag{11}$$

The last equation gives the lifetime detection probability as a function of the annual detection, δ, and annual return, $\Phi = \sigma\rho$.
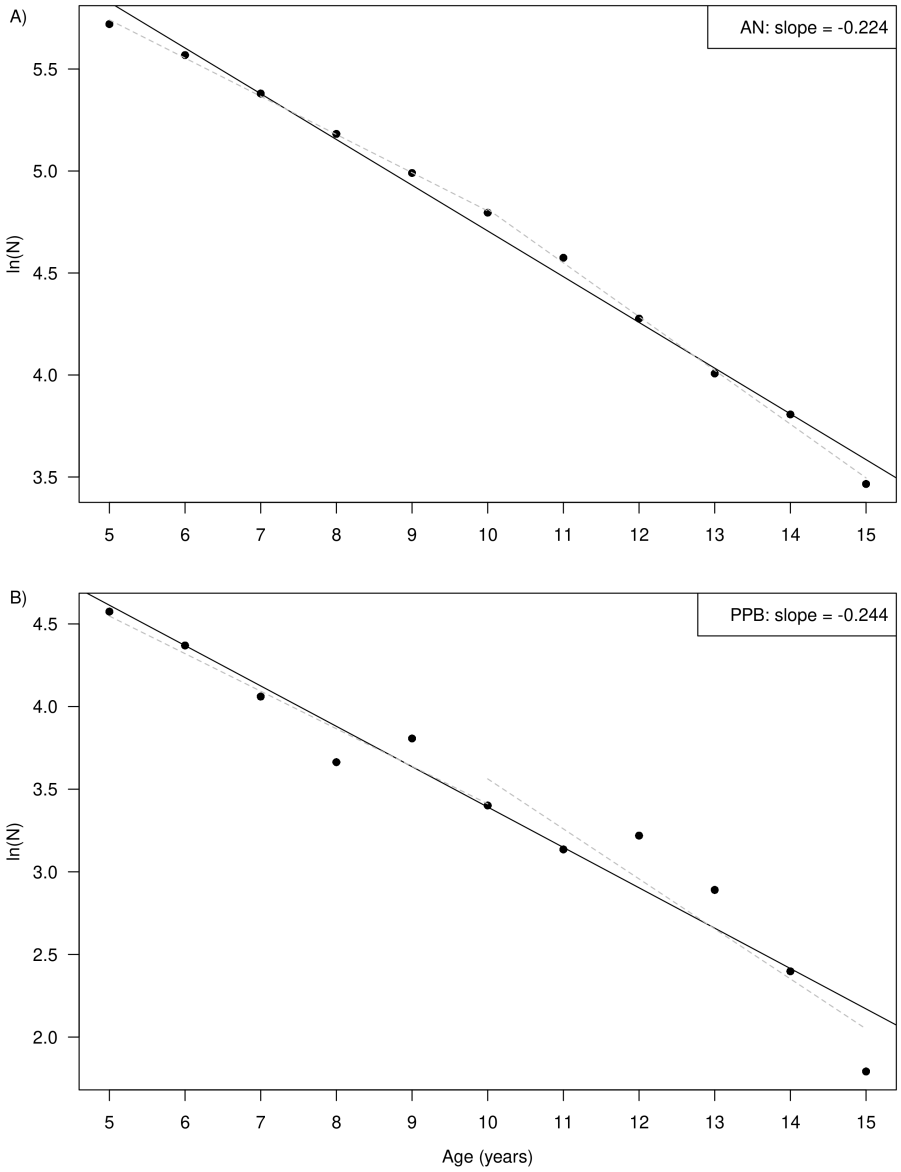
Figure S1. Decline in number of observed females on a colony with age. The vertical axis gives the natural log of the number of animals observed at each age, combining cohorts 1994-2010. The horizontal axis is female age in years; ages 5-15 include the main breeding life, when fecundity is at its maximum and before senescence. A) Año Nuevo (AN). B) Piedras Blancas (PPB). The slopes shown are estimates of $\ln \sigma$, the logarithm of the rate of reappearance (see Appendix S2), thus $\sigma = 0.799$ at Año Nuevo (confidence interval 0.788-0.810), $\sigma = 0.783$ (0.754-0.814) at Piedras Blancas. At each colony, a separate slope was fitted using ages 5-10 and again ages 10-15 (dashed gray lines). In both cases, the second slope was steeper, but in neither case did it differ statistically from the first.