

Article

Minimizing Potential Allee Effects in Psittacine Reintroductions: An Example from Puerto Rico

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Abstract: The family Psittacidae is comprised of over 400 species, an ever-increasing number of which are considered threatened with extinction. In recent decades, conservation strategies for these species have increasingly employed reintroduction as a technique for reestablishing populations in previously extirpated areas. Because most Psittacines are highly social and flocking species, reintroduction efforts may face the numerical and methodological challenge of overcoming initial Allee effects during the critical establishment phase of the reintroduction. These Allee effects can result from failures to achieve adequate site fidelity, survival and flock cohesion of released individuals, thus jeopardizing the success of the reintroduction. Over the past 20 years, efforts to reestablish and augment populations of the critically endangered Puerto Rican parrot (*Amazona vittata*) have periodically faced the challenge of apparent Allee effects. These challenges have been mitigated via a novel release strategy designed to promote site fidelity, flock cohesion and rapid reproduction of released parrots. Efforts to date have resulted in not only the reestablishment of an additional wild population in Puerto Rico, but also the reestablishment of the species in the El Yunque National Forest following its extirpation there by the Category 5 hurricane Maria in 2017. This promising release strategy has potential applicability in reintroductions of other psittacines and highly social species in general.

Keywords: Psittacidae; reintroduction; Allee effect; population; survival; reproduction; site fidelity; flock cohesion



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1. Introduction

The family Psittacidae is comprised of over 400 species, an ever-increasing number of which are considered threatened or endangered [1,2]. In recent decades, conservation strategies for these species have increasingly employed reintroduction as a technique for reestablishing populations in previously extirpated areas [2–5]. However, reintroductions in general face substantial biological and methodological challenges, and many are ultimately unsuccessful [2,3,6,7]. Among these challenges are inherent—but often overlooked—Allee effects associated with small populations [7–10]. Allee effects are generally considered as consisting of either component effects (i.e., those which affect a component of individual fitness), or demographic effects, which affect per capita growth rates at the population level [11]. Examples of Allee effects include increased per capita predation risk, reduced foraging efficiency, and reduced pair-formation and reproductive effort, all of which contribute to reduced population growth [7–9]. These effects are particularly notable in group-living social species [9,11]. For example, the viability

of African wild dog (*Lycaon pictus*) populations declines markedly once group size falls below a critical threshold, as also occurs with schools of bluefin tuna (*Thunnus thynnus*) and social groups of suricates (*Suricata suricatta*) [9]. Although Allee effects typically are considered as affecting populations as they decline from previously robust levels, in recent years, component and demographic Allee effects have increasingly been recognized during the establishment phase of reintroduced populations, before population size has achieved a robust, sustainable level [9,12–14]. Because most psittacines are highly social and flocking species, reintroduction efforts may face the numerical, behavioral and methodological challenges of minimizing initial Allee effects during the critical establishment phase of the reintroduction [9,14–16]. For example, although Snyder et al. [3] did not explicitly identify a component Allee effect as affecting releases of Thick-billed parrots (*Rhynchopsitta pachyrhyncha*) in Arizona, USA, they clearly implied such by stating that there appeared to be a “critical mass” of group size that conferred greater protection to released birds from avian predators. Further, Brightsmith et al. [4] reported that post-release survival of hand-reared Scarlet macaws (*Ara macao*) increased with increasing cohort sizes, and that macaws established at release sites facilitated survival of subsequent releases, also suggestive of a potential component Allee effect. Common challenges of reintroducing psittacines include, but are not limited to: (1) excessive or premature dispersal from the release area, (2) maintaining flock cohesion, (3) maximizing survival, and (4) obtaining reproduction rapidly following release [3,14,17–20]. If these challenges are not recognized and adequately addressed or ameliorated, they can result in failed efforts and wasted resources [2,3,9,13,15,16]. Management efforts for meeting these challenges typically fall into three general categories: (1) managing release group size and composition, (2) reducing post-release dispersal and mortality, and (3) direct management of Allee effects (e.g., predator control, supplemental feeding) [9,16].

The Puerto Rican parrot (*Amazona vittata*) is a critically endangered psittacine endemic to the island of Puerto Rico, for which an ongoing species conservation and recovery program has existed since the early 1970s [17,18]. Like most psittacines, Puerto Rican parrots are primarily frugivorous canopy-dwellers, secondary cavity nesters, and also exhibit marked natal philopatry and nest-site fidelity [17,18]. The total wild population has remained precariously low throughout the recovery program, ranging from a low of 13 to nearly 200 individuals over the period 1973–2017 [17,18] (USFWS, unpubl. data). Since 2000, captive-reared parrots have been released under a variety of scenarios in order to augment the sole relict wild population of the species in the El Yunque National Forest (hereafter EYNF), and to reestablish the species at an additional location on the island (i.e., Rio Abajo Commonwealth Forest) [17,20–23]. Moreover, future releases to reestablish the species at yet a third location (i.e., Maricao Commonwealth Forest) are anticipated. Here, we examine these scenarios, specifically those related to the relict population in the EYNF, in terms of how and why specific release strategies have achieved the desired objectives and potentially minimized some of the inherent initial Allee effects often associated with reintroduced populations [9,12,14,16]. We believe our findings have direct relevance to reintroductions of not only psittacines, but also other highly social or group-living species. We use the term “reintroduction” herein in its broadest sense, inclusive of all its recognized variants [2,24].

2. Materials and Methods

We examined and compared four (4) distinct captive release strategies in terms of their efficacy in establishing a resident, breeding population of Puerto Rican parrots. These strategies included: (1) Soft release of individual groups of captive-reared parrots translocated to a wild release site (hereafter “traditional release”); (2) Hard release of small numbers of captive-reared parrots translocated directly to a wild release site (hereafter “precision release”); (3) Soft release of multiple groups of captive-reared parrots translocated to a wild release site with conspecifics held on-site briefly following release (hereafter “soft release type A”); (4) Soft release of captive-reared parrots released on-site at a captive-

breeding facility (hereafter “soft release type B”). In the context of this study, the term “soft release” refers to those methods that include on-site acclimation at the release site, and post-release support or supplementation. “Hard release” refers to methods involving no on-site acclimation, and no post-release support [8]. All parrots were released in the EYNF of northeastern Puerto Rico (approx. 18.32° N; 65.78° W, Figure 1), a mountainous forest reserve consisting of 19,650 ha of subtropical rainforest at elevations ranging from 200 to 1074 m ASL [20]. However, all releases occurred at elevations ranging from 500 to 700 m ASL, in the Tabonuco and Palo Colorado forest types [18,20], within the subtropical montane rainforest life zone [18,20]. Detailed descriptions of all forest types in the EYNF are found in Snyder et al. [18].

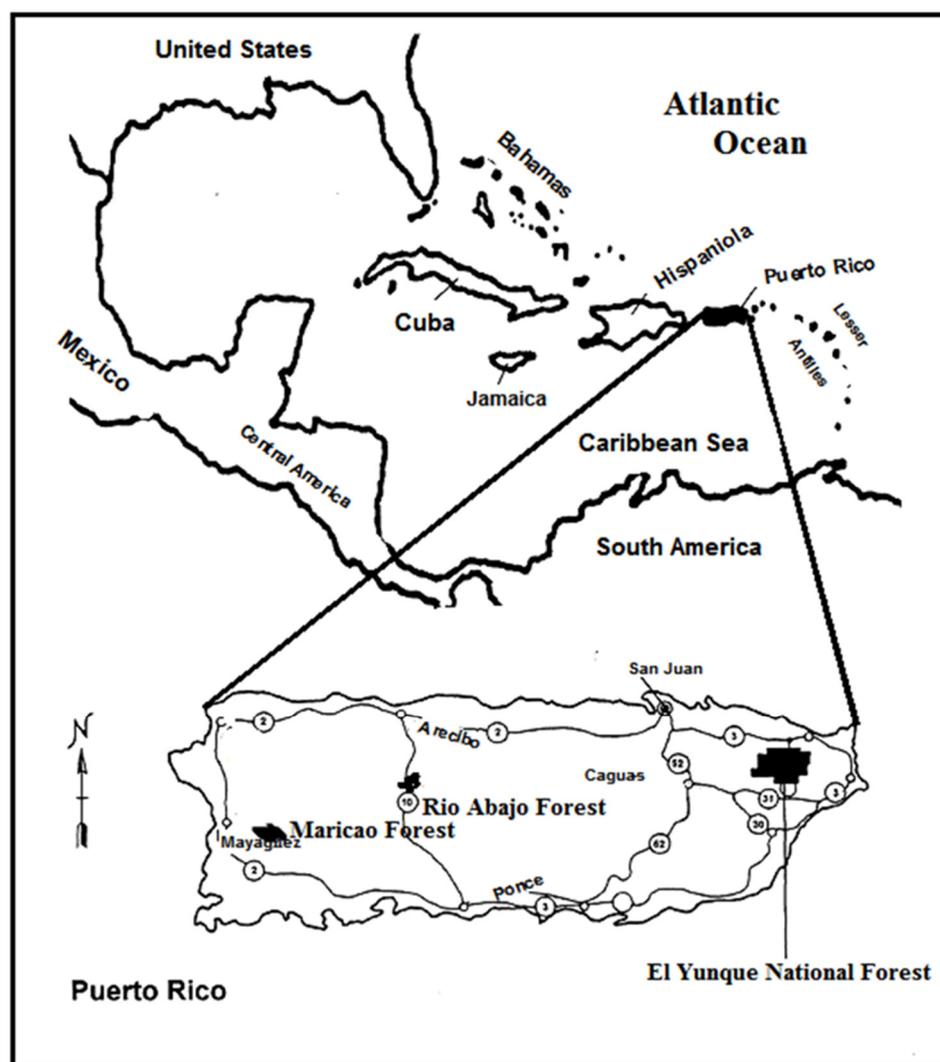


Figure 1. Location of Puerto Rico within the Caribbean Basin, and locations of the El Yunque National Forest and Rio Abajo Commonwealth Forest (sites of current wild Puerto Rican parrot populations) and the Maricao Commonwealth Forest, where future releases of Puerto Rican parrots are planned for reestablishing the species at a third location.

2.1. General Release Methodologies

2.1.1. Traditional Release

“Traditional release” is the most common release method for captive-reared animals in the reintroduction literature, e.g., [3,8,19,20]. For the Puerto Rican parrot, this consisted of rearing a group (15–20) of parrots together to desired age of release (1–4 years of age), and providing pre-release flight training, wild foods (>50 species) and predator aversion

training for a minimum of 6 months in large (approx. 9 m × 8 m × 5 m) outdoor flight cages. Because the parrots were to be monitored post-release using radio-telemetry, replica “dummy” radio transmitters were attached to all release candidates during pre-release training to accustom them to flying and foraging with the device prior to release [19–21]. Flight cages were equipped with both stable and non-stable perches comprised of natural materials. Natural wild foods were offered in the same fashion as parrots would encounter in the wild. Complete fruiting branches, racemes, etc., were suspended from perches and cage roofs and sides to accustom birds to identifying and manipulating these foods in the wild. Following the initial training period, parrots were transported to a release cage for on-site acclimation (30–40 days) at a release site occupied by wild conspecifics [20]. All parrots were equipped with a functioning radio-transmitter (Holohil®, Ottawa, ON, Canada, SI-2C model) approximately 5–7 days prior to release to allow monitoring of their movements and survival post-release. Immediately following on-site acclimation, all parrots were allowed to exit the release cage at will. All releases occurred at dawn. Supplemental food sources were provided daily at the release site for a period of 2–4 weeks following release. Following each release, parrots were radio-tracked 3–5 days/week for the duration of transmitter life (approx. 10–16 months), or parrot mortality. The traditional releases occurred in EYNF at the end of the wild parrot nesting season (June) during 2000–2002 and 2004 [17,20]. Because of numerous predations of released parrots and wild parrot fledglings by Red-Tailed Hawks (*Buteo jamaicensis*) during 2000–2002, active predator control was implemented within 1.5 km of the release site, beginning in 2003, and continued throughout all subsequent years for all releases [17,20].

2.1.2. Precision Release

“Precision release” was an experimental methodology aimed at the fostering rapid integration of limited numbers of captive-reared parrots into an existing population. Like traditional releases, all release candidates were provided with at least six months of extensive pre-release training. However, unlike traditional releases, only two individuals were released during any given release event. All parrots released ranged from 1–2 years in age. Moreover, each release occurred within 100 m of an active wild parrot nest site, immediately (1–2 days) following fledging of the last nestling from the nest (typically May–June [17,18]). Releases were thus timed to take advantage of the early post-fledging phase, during which wild Puerto Rican parrot family groups remain relatively sedentary for several days, and with greatly diminished nest site territoriality [18]. The objective was to promote greater and more rapid interaction between wild and released parrots than had been observed following traditional releases [20]. All parrots so released were transported directly from the captive-rearing facility and released immediately at the wild nest site shortly after dawn, with no post-release supplemental food sources provided. Each parrot was also equipped with a radio-transmitter to allow post-release monitoring. Precision releases occurred in EYNF in alternate years from 2008 to 2010, and then yearly thereafter until 2014.

2.1.3. Soft Release Type A

“Soft release type A” was also an experimental release methodology. The objective was to promote increased site fidelity and flock cohesion of the release cohorts, as well as social interactions between the relict wild population and the released captive-reared birds. As with both the traditional releases and precision releases, all release candidates underwent at least 6 months of extensive pre-release training prior to transport to the release site. Parrots released ranged from 1 to 3 years of age. During pre-release training, candidates were closely observed for signs of potential pair bonds developing (e.g., allopreening, allofeeding). The use of unique color and shape-coded tags facilitated identification of individual parrots during training. Soft release type A also involved a 30–40 day on-site acclimation period at the release site (as with traditional releases), following which the parrots were released in two (2) groups over a period of 6–8 days. The release cage was

divided into two equal-size segments to allow release group separation. Group 1 consisted of the males of any apparent pairs, together with a mix of unpaired males and females, and was released first. Group 2 consisted of the females of apparent pairs, together with a mix of other unpaired males and females, and released 6–8 days following Group 1. All releases occurred at dawn, and parrots were allowed to exit cages at will. Once all parrots had vacated both release cages, the following morning an additional group of 6–8 captive-reared parrots was placed in one of the release cages for a period of 2–3 weeks to serve as an additional “social attractant” for the newly released parrots. Supplemental food sources were provided and replenished daily at the release site for at least one year following release. All parrots were equipped with radio-transmitters to allow post-release monitoring. The soft release type A releases occurred in EYNF at the end of the wild parrot nesting season (June) during 2015–2017.

2.1.4. Soft Release Type B

“Soft release type B” releases were conducted on the grounds of the two captive-rearing facilities for the species, one of which is in the Rio Abajo Commonwealth Forest (hereafter, RAF) in northcentral Puerto Rico and the other in the EYNF [17,22,23]. At each of these facilities, a large number (currently 225–275) of captive-reared Puerto Rican parrots are housed and maintained in outdoor cages in a natural setting. Because the objective of these releases was to reestablish a free-flying wild population in an area from whence it had previously been extirpated, these releases were true “reintroductions” as defined by IUCN guidelines [24]. As with the other release strategies for the species, all release candidates received at least 6 months of extensive prerelease training, with some individuals receiving up to one year of training. As with soft release type A, parrots for release in EYNF ranged from 1 to 3 years of age, with the exception of one individual of six years of age. The 6-year-old parrot was a parrot previously released in 2015, which returned to the captive rearing facility following hurricane Maria in 2017. However, unlike soft release type A, all birds of soft release type B were reared and trained at the actual release site, and released directly from the prerelease training cage, instead of being transported to a separate release site. As with other releases, all parrots were equipped with radio transmitters to allow post-release monitoring. Upon release, supplemental food sources were provided daily near (10–30 m) the release site, and maintained continuously following each release. Several (8–10) artificial nest cavities [25] were also strategically placed within the release area in order to provide immediate nesting opportunities for the parrots following release. Soft release type B releases occurred during November 2006 at RAF [23] and January/February 2020 at EYNF, immediately prior to the species’ normal nesting season (February–June).

2.2. Data Analyses and Reporting

We report and discuss the results of each type of release in EYNF in terms of four key parameters we considered important for successful reestablishment of psittacine populations: (1) survival, (2) site fidelity, (3) flock cohesion, and (4) prompt reproduction. We define “prompt reproduction” as successful reproduction by parrots within 18 months post-release, expressed as the proportion of surviving breeding age (≥ 3 years) parrots that successfully nested during this period. We choose 18 months as a temporal benchmark as it allows all release cohorts time to adapt to the release environment and experience at least one complete nesting season following release, independent of their actual month of release. We considered prompt reproduction important in the context of establishing a resident population. This is because wild Puerto Rican parrots exhibit an annual philopatry of 87.5% to previously successful nesting sites [18,26]. Thus, prompt reproduction may more quickly and effectively “anchor” released individuals in the release area. We define “site fidelity” as the percentage of released parrots that established a stable activity area within 1.5 km of the release site, excluding any temporary longer distance forays. We choose 1.5 km as a spatial delineator because it corresponds to the radius of the primary area utilized by the relict wild Puerto Rican parrot population in EYNF during the last two decades,

prior to their extirpation by the Category 5 hurricane Maria in 2017 (USFWS, unpublished data). We define “flock cohesion” as the percentage of surviving individuals that directly interacted (e.g., flying, foraging, roosting) as a group within the release area. With the exception of soft release type B, this also includes any direct interactions with, or integration into, groups of wild conspecifics at or near the release site. We report “survival” as the percentage of released individuals that survived for at least one year post-release [17,20]. Additionally, because most post-release mortalities of captive-reared psittacines occur within the first three months (90 days) after release ([3,17,19,20,27]; see [4,28]), we also report initial 3-month post-release survival for each release type. We estimated weekly, 3-month and annual survival of soft release types A and B in EYNF using the Kaplan–Meier product-limit estimator, in order to directly compare with published survival estimates for “traditional” captive releases of this and similar species [17,19,20], and because there were occasional censored observations (i.e., missing individuals and/or transmitter failures) during these releases. Censored observations were more frequent following soft release type B in EYNF due to personnel limitations and restrictions associated with the ongoing COVID-19 global pandemic, which resulted in reduced monitoring intensity compared to that of previous releases. For precision releases, because of the very low sample sizes ($n = 2$ individuals/release) for each of the multiple releases of this type, we report the overall range and average known survival pooled across all releases, as these releases did not meet the sample size requirements for Kaplan–Meier methods [19]. Finally, because of the distinct differences in release area habitat and microclimate between RAF and EYNF [17,18], we also report and discuss the first-year survival results of RAF soft release type B [23] for comparative purposes only. We did this in order to eliminate an additional and unquantifiable source of variability in the overall results, and facilitate a more accurate and direct comparison of the actual release strategies without the confounding effects of habitat or environmental differences. All percentages reported were rounded to nearest percent for simplicity. Kaplan–Meier first-year survival estimates are reported with associated 95% confidence intervals (CI), and compared using a log-rank test [29]. Differences in survival trajectories were considered significant at $\alpha < 0.05$.

3. Results

3.1. Traditional Releases

3.1.1. Survival

A total of 39 captive-reared parrots were released in EYNF using traditional releases from 2000 to 2004 [17]. As previously reported see [17,20], overall first-year survival for traditional releases was 41% (CI: 22–61%), whereas survival at three months post-release was 74% (see [20], Figure 2). Similar traditional releases of captive-reared Hispaniolan parrots (*A. ventralis*) in the Dominican Republic resulted in a first-year survival of 30%, with a 3-month post-release survival of 60% [19]. In the EYNF, raptor predation was responsible for at least 53% (9/17) of the documented mortalities [17]. The causes of the remaining mortalities could not be determined, although additional raptor predations were possible [20]. Interestingly, most (67%) of the raptor predations occurred following increased dispersal of individual parrots from the release area approximately 6–8 weeks post-release (see [17] (pp. 22, 49)).

3.1.2. Site Fidelity

According to White et al. [20], individual parrots began dispersing from the immediate release area approximately two months following each release. Dispersing parrots often travelled up to 6–8 km from the release site (USFWS, unpublished data). All parrots which so dispersed did not return to the release area (i.e., 1.5 km radius of release site), and most were later recorded as mortalities or censored observations [20]. On one occasion, a pair (male, female) of released parrots returned to the captive-rearing facility, approximately 3 km from the release site, 11 months post-release. These parrots also did not return to

the release area. Overall, site fidelity for traditional releases was low, with approximately 30–40% of released parrots remaining within the release area one year post-release.

3.1.3. Flock Cohesion

As with site fidelity, flock cohesion of traditional release cohorts was low. Few (approximately 20–25%) of the surviving parrots that remained within the release area for up to one year post-release were observed engaging in typical flocking behaviors with either wild or other released captive-reared parrots.

3.1.4. Prompt Reproduction

There was no successful reproduction (or attempts at such) by traditionally released parrots within 18 months post-release, despite the fact that several parrots (44%) were released at or entering breeding age within said period [20]. According to White et al. [20], there were documented nesting attempts by only three traditionally released parrots. These attempts first occurred in 2004 and consisted of a pair of captive-reared parrots released in 2002 at the ages of one and two years. This attempt was unsuccessful, and no subsequent nesting attempts by this pair were documented. The other was a captive-reared male released in 2001 at the age of one year, which successfully nested with a wild female and fledged two chicks in 2004 [20]. This pair continued to successfully nest each year thereafter until the disappearance of the male in 2009.

3.2. Precision Releases

3.2.1. Survival

A total of 36 captive-reared parrots were released in 18 separate release events in EYNF during six different years. Overall first-year survival of precision releases averaged 59%, although it ranged widely from 25% to 75% annually. Survival at three months post-release averaged 76%, while also ranging annually from 50% to 87%. Although raptor predation was confirmed as a cause of mortality in at least six (40%) cases, the cause of most mortalities remained unknown due to their occurrence in inaccessible areas, which precluded recovery of transmitters or parrot remains. In such cases, mortality was presumed when parrot movements ceased and transmitters remained stationary thereafter. We based this presumption on past experience with radio-tracking parrots in this environment [17,20].

3.2.2. Site Fidelity

Site fidelity of precision releases was markedly low. Released parrots typically remained near (<200 m) the release site for 2–5 days post-release, and then rapidly engaged in extensive movements both within and outside the immediate release area (USFWS, unpublished data). These movements also include the longest distances documented by captive-reared parrots released in EYNF, many of which resulted in parrot locations within suburban and urban areas up to 23 km from the EYNF release site. On four separate occasions, a precision released parrot returned to the captive-rearing facility, and did not return to the release area. Indeed, of 21 parrots known to have survived for one year, only 8–10 (38–48%) were subsequently observed within the release area. Thus, only 22–28% of all precision released parrots during 2008–2014 remained within the release area after one year.

3.2.3. Flock Cohesion

Flock cohesion of precision released parrots was relatively low. Although most released parrots exhibited some initial vocal interactions with both wild and previously released parrots (T. White, pers. observation), there were few instances (4–6) of their long-term integration into existing groups of resident birds. Nevertheless, it was notable that there were no agonistic interactions witnessed between released parrots and wild parrots, despite the fact that parrots were released in close proximity (<100 m) to family groups

of newly fledged wild parrots (T. White, pers. Observation). Released parrots were also occasionally seen flying with or towards wild parrots during the initial days post-release.

3.2.4. Prompt Reproduction

Not surprisingly, given the very low site fidelity and flock cohesion, there were likewise no cases of prompt reproduction by precision released parrots with either wild parrots or other captive-reared parrots. Notwithstanding, during 2014, a male parrot that had been precision-released in 2012 was observed nesting with a wild female (USFWS, unpublished data). This pair successfully fledged three chicks from an artificial nest cavity that year. Unfortunately, that was the only year this particular male was observed nesting, and his subsequent fate remains unknown.

3.3. Soft Release Type A

3.3.1. Survival

A total of 65 captive-reared parrots were released during 2015–2017; with 20, 24 and 21 being released in 2015, 2016, and 2017, respectively. Overall first-year survival of soft release type A releases (2015, 2016) was 64% (CI: 50–79%; Figure 2), while initial 3-month survival averaged 85% (all three cohorts). No first-year survival data exist for the year 2017 release cohort, as virtually the entire wild population in EYNF was extirpated by hurricane Maria approximately 12 weeks following the 2017 release. However, at the time of the hurricane (20 September 2017), survival of the 2017 cohort was 95% (USFWS, unpublished data).

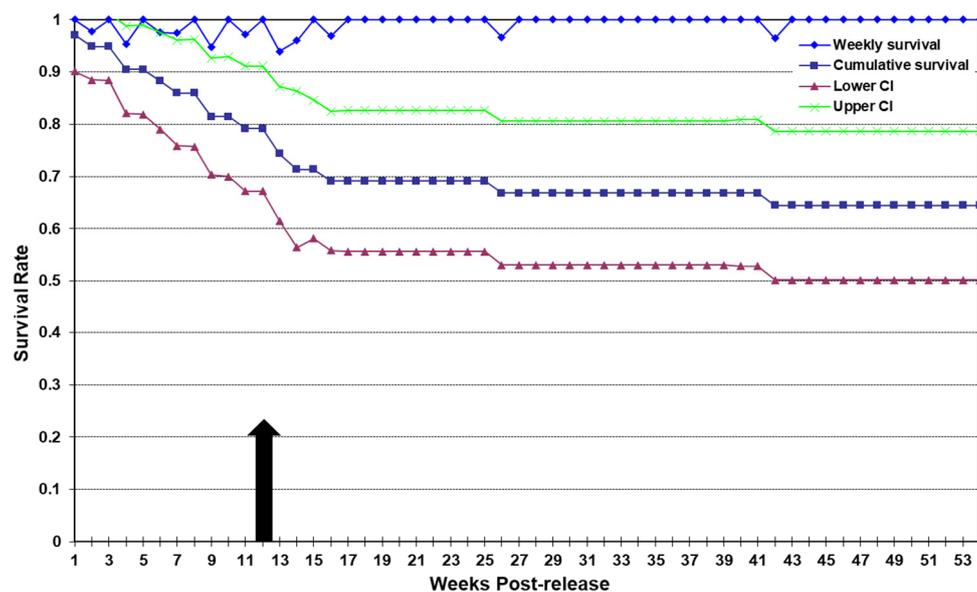


Figure 2. Kaplan–Meier weekly and cumulative survival estimates for 44 captive-reared Puerto Rican parrots released during soft release type A in the El Yunque National Forest, Puerto Rico, 2015–2016. Black arrow denotes 3-months post-release.

3.3.2. Site Fidelity

Site fidelity of soft release type A parrots was comparatively high. All surviving parrots remained within the release area following release, despite occasional longer distance forays by some individuals lasting from 2 to 4 days. All parrots who engaged in such forays later returned to the release area. Thus, the locations and status of most released parrots were known each day of monitoring, and there were few censored observations except for a single week in 2015, when a predation attempt at the release site by a Red-tailed hawk resulted in the rapid dispersal of over 50% of the released birds from the area. However, all dispersed parrots returned to the release area within five days.

3.3.3. Flock Cohesion

As with site fidelity, flock cohesion by soft release type A parrots was very high. All surviving parrots of each release event interacted on a daily basis with not only members of their release cohort, but also parrots of other release cohorts. Moreover, approximately four months post-release, beginning in 2015, released parrots and wild parrots were observed and video-recorded directly interacting at the release site (location of supplemental feeders) and within the surrounding area. These interactions consisted of vocal exchanges as well as flying and foraging together on wild foods. Interestingly, wild parrots were never observed approaching or utilizing supplemental feeders, despite the fact that they (wild birds) would often perch in the canopy immediately above supplemental feeders being used by released parrots.

3.3.4. Prompt Reproduction

Reproduction by soft release type A parrots began the first breeding season (<1 year) following release. A pair of captive-reared parrots released in June 2015 nested and fledged two chicks during both the 2016 and 2017 breeding seasons, in addition to a pair released in 2016 that also nested and fledged three chicks during the subsequent 2017 season. Thus, there were three successful nesting attempts during the first 18 months post-release. For parrots released in 2015 and 2016, this represented 18% and 17%, respectively, of the total breeding-age birds released each year. Two additional pairs of captive-reared parrots were observed engaging in stereotypical nesting behavior (e.g., allofeeding, defending and entering nest cavities) during the 2017 season, but did not actually nest.

3.4. Soft Release Type B

3.4.1. Survival

A total of 30 captive-reared parrots were released in EYNF during late January-early February 2020. As with soft release type A, captive-reared parrots were released in two groups; one group of 15 birds on January 30 followed by a second group of 15 birds on February 6. To date (i.e., 10 months post-release), the survival estimate is 68% (CI: 47–87%, Figure 3). Three-month (12-weeks) post-release survival of this cohort was 94% (Figure 3), very similar to the 92% survival reported by Estrada [5] for Scarlet macaws released in Mexico. The greatest declines in overall survival occurred 24–26 weeks and 41–42 weeks post-release (Figure 3), when at least six parrots were lost to raptor predations during two separate episodes. Survival of type B releases was higher than that of traditional releases ($\chi^2 = 8.779$, $df = 1$, $p = 0.003$), but not significantly greater than type A releases ($\chi^2 = 0.792$, $df = 1$, $p = 0.373$). However, early post-release survival of type B releases was much higher than that of type A during the ensuing breeding season over the 20 weeks immediately following the type B release ($\chi^2 = 7.647$, $df = 1$, $p = 0.006$; Figure 4).

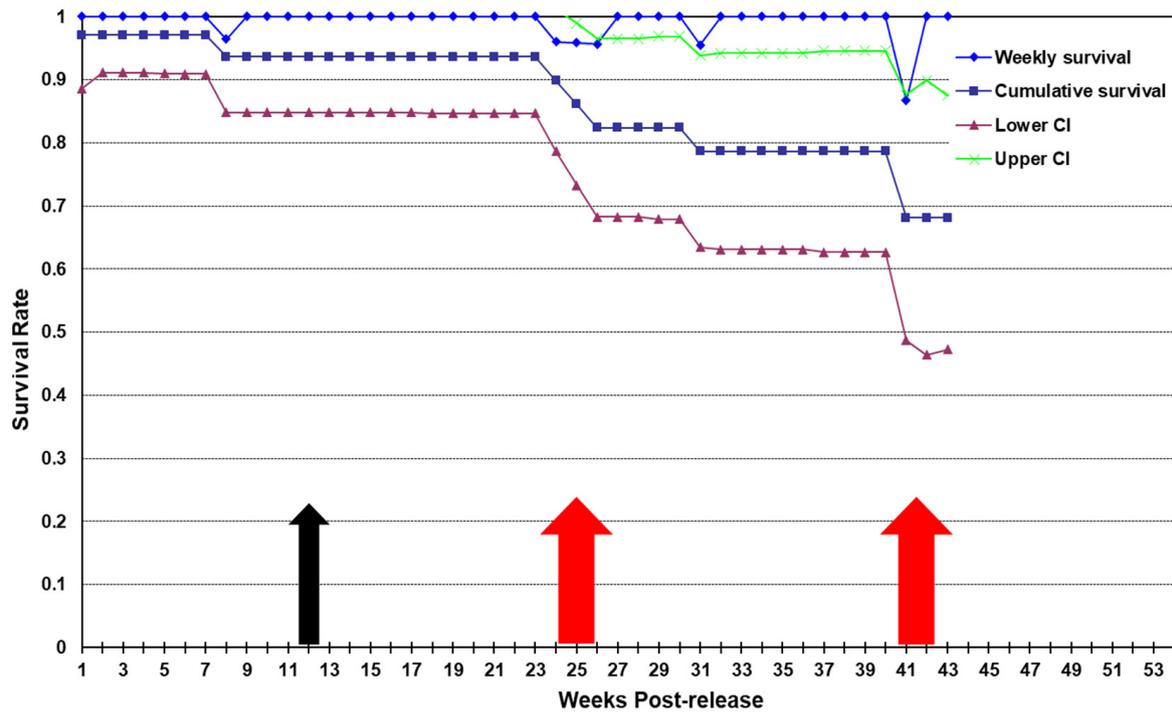


Figure 3. Kaplan–Meier weekly and cumulative survival estimates for 30 captive-reared Puerto Rican parrots released during a soft release type B in the El Yunque National Forest, Puerto Rico, 2020. Black arrow denotes 3-months post-release. Red arrows denote 24–26 weeks and 41–42 weeks post-release, corresponding to two episodes of raptor predation of several released parrots near release site, which accounted for 75% of all documented post-release mortalities.

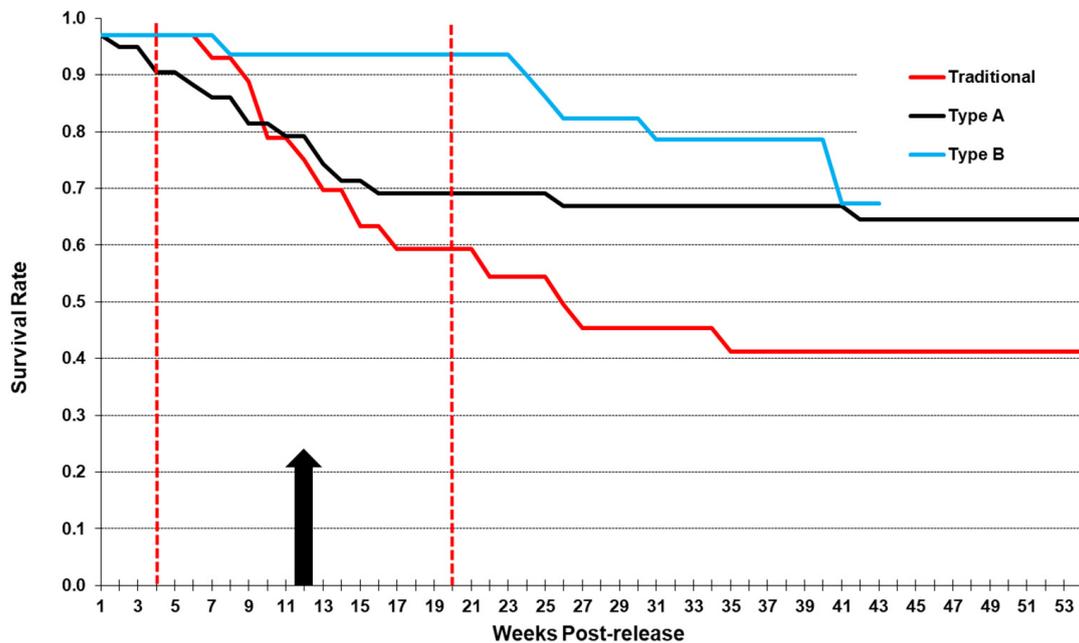


Figure 4. Comparison of survival trajectories based on Kaplan–Meier survival estimates for traditional, type A, and type B releases of captive-reared Puerto Rican parrots in the El Yunque National Forest, Puerto Rico, 2000–2020. Survival trajectory of traditional releases adapted from White et al. [17,20] and used with permission. Vertical red lines delineate temporal span (approx. 16 weeks) of the species’ reproductive season. Black arrow denotes 3-months post-release.

3.4.2. Site Fidelity

Site fidelity of released parrots was moderately high. Of the 30 birds released, 26 (87%) remained within the release area until 24–26 weeks post-release, when a series of raptor attacks resulted in the temporary dispersal of several individuals from the area. Although most of the dispersed parrots later returned to the release area, two did not and their current locations are unknown. Approximately 10 months (40 weeks) post-release, 20 (67%) of the released parrots remained within the release area and immediate vicinity of the release site, until a second episode of raptor attacks during weeks 41–42 resulted in the dispersal of several parrots and additional censored observations.

3.4.3. Flock Cohesion

As with site fidelity, flock cohesion of soft release type B parrots was high. Virtually all (95%) of the surviving parrots remained together as a flock within the release area. Moreover, parrots were observed daily flying and foraging together, and engaging in group antipredator behaviors (e.g., posting “sentinels” while foraging, coordinated flights to confuse raptors) [30].

3.4.4. Prompt Reproduction

Reproduction by soft release type B parrots was very rapid, with two pairs of released parrots initiating nesting activities within two months of release. This represented 25% of the total number ($n = 16$) of breeding-age birds released (Table 1). Interestingly, the male of one breeding pair was a 6-year-old parrot that was, at the time of release, the sole surviving individual of the former wild population prior to hurricane Maria (Figure 5). Both pairs successfully fledged chicks, with one pair fledging three chicks and the other two. Indeed, this was the most rapid reproduction of captive-released parrots ever documented for this species. As occurred with the soft release type A releases, there were two additional pairs that engaged in stereotypical nesting behaviors post-release, but failed to actually nest. In both of these cases, at least one member of the pair was only two years of age, and thus unlikely to be sexually mature [18]. A graphical comparison of summary statistics for all four release types is presented in Figure 6.

Table 1. Summary statistics for four different types of release for captive-reared Puerto Rican parrots in the El Yunque National Forest, Puerto Rico, 2000–2020. Site fidelity refers to percentage of released parrots that remained within 1.5 km of release site; Flock cohesion refers to percentage of surviving parrots that remained in release area interacting as a group; Prompt reproduction refers to percentage of reproductive age parrots released that successfully nested within 18 months post-release.

Release Type	Survival 1-Year	Site Fidelity	Flock Cohesion	Prompt Reproduction
Traditional	41%	30–40%	20–25%	0
Precision	59%	22–28%	11–17%	0
Soft Release A	64%	65%	100%	18%
Soft Release B	68% ¹	67% ¹	95% ¹	25%

¹ 10 months post-release (November 2020).



Figure 5. Pair of captive-reared Puerto Rican parrots (male–upper; female–lower) released during a soft release type B in the El Yunque National Forest, 30 January 2020. The pair began nesting at this artificial nest cavity 29 February 2020 (30 days post-release) and subsequently fledged three chicks from this nest. This was the first active nest of free-flying parrots in the El Yunque National Forest following hurricane Maria in 2017. Photograph taken by Thomas White.

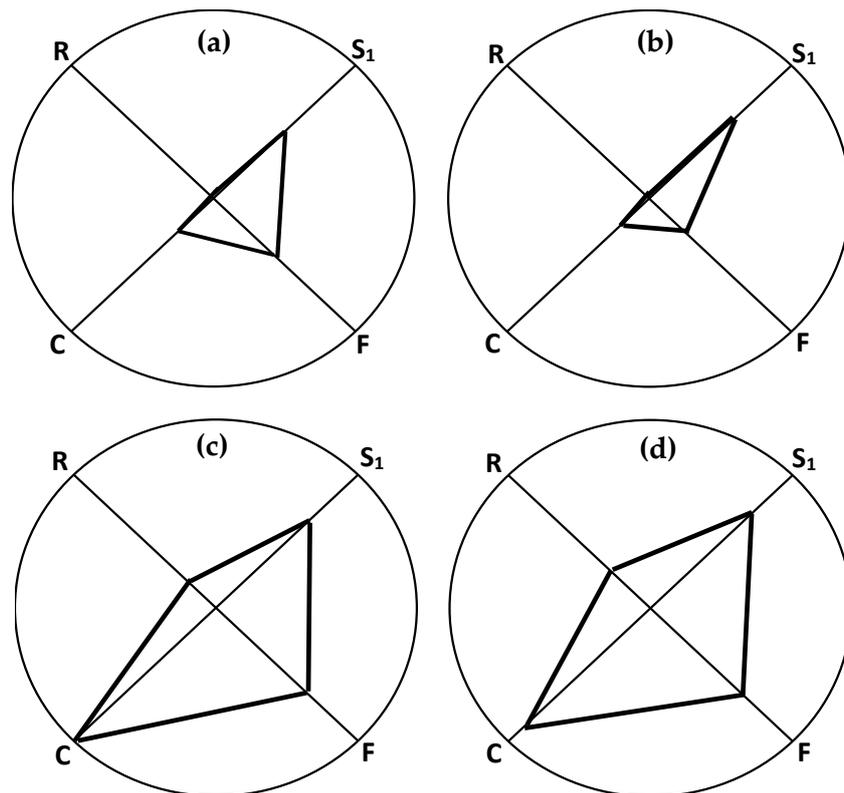


Figure 6. Graphical representation of the relative efficacy of four different strategies for establishing a resident breeding population of Puerto Rican parrots from captive-reared individuals in the El Yunque National Forest, Puerto Rico, 2000–2020. R-axis is prompt reproduction, S_1 -axis is first-year survival, F-axis is site fidelity, C-axis is flock cohesion. Circumference of circle represents 100%, while intersect at center represents zero for associated axial parameter values. Area of interior polygons indicates degree of maximization of the four component parameters. Release types depicted: (a) Traditional release, (b) Precision release, (c) Soft release type A, (d) Soft release type B.

4. Discussion

We examined the results of four different strategies for the release of captive-reared Puerto Rican parrots during 26 distinct release events totaling 170 parrots from 2000 to 2020 in the El Yunque National Forest in Puerto Rico. Because the fundamental pre-release training of all released parrots was the same, we were able to compare the actual release strategies and methodologies in terms of their effectiveness at promoting survival, site fidelity, flock cohesion and prompt reproduction by released parrots. We believed these parameters to be important in mitigating or reducing potential Allee effects associated with small populations, as commonly occurs during the initial establishment phase of reintroductions [9,16]. As such, our study adds to the findings of White et al. [2] regarding factors influencing the success of psittacine reintroductions. Although survival is the single most commonly reported parameter of reintroduction attempts (e.g., [2,4,19,20,28]), site fidelity and flock cohesion are seldom addressed explicitly, as reported in this study. However, these parameters are all inextricably interrelated when reintroducing highly social species [14,16].

For captive-reared Puerto Rican parrots released in the EYNF, post-release survival tended to increase not only with the size of release cohorts, but also with numbers of conspecifics at or near the release site. This was particularly apparent in the case of soft release type B in EYNF (Figure 4), in which the largest release of parrots ($n = 30$) occurred, and in the presence of approximately 250 captive conspecifics held in outdoor cages at the release site. Indeed, of the four release methods, soft release type B resulted in improved post-release survival (Table 1, Figures 3 and 4), with a 3-month survival of 94%. In comparison, Llerandi-Román et al. [23] reported a first-year survival of 48% for a similar soft release type B in the RAF. Although post-release survival of type B eventually (approx. 10 months post-release) approximated that of type A releases, the initial survival during the critical early establishment phase and concomitant reproductive season was very high (>90%) throughout the season (Figure 4). In a previous study of factors associated with success of psittacine reintroductions, White et al. [2] did not find these factors (i.e., numbers released, conspecifics present) to be significant, perhaps due to the high variability in this parameter among those reintroductions examined. Nevertheless, many other studies have found positive relationships between numbers released and establishment success ([6,31,32], but see [16] for some caveats). In this study, we believe the presence of a large number of conspecifics held on-site aided newly released parrots in terms of more effective predator detection and avoidance. This was because, having been held in outdoor cages, all captive parrots had substantial prior exposure to avian predators, and most had even witnessed raptor predations of other avian species (e.g., *Zenaida* spp.) at the captive-rearing facility (T. White, pers. observations; see also [28]). These numerous captive “sentinels” quickly sounded alarm calls that alerted released parrots to impending dangers (T. White, pers. observation), thereby increasing the “effective flock size” of released parrots in terms of predator detection and avoidance [29]. We believe this increase in effective flock size helped to mitigate or reduce per capita risk associated with a potential predator-driven Allee effect, as suggested by White et al. [17] and demonstrated theoretically by Gascoigne and Lipsius [33] and empirically by Angulo et al. [34]. This is very important because the primary source of mortality for parrots in the EYNF has historically been raptor predation ([17,18,20], this study). Following soft release type B, survival trajectories (weekly, cumulative) were characterized by high survival for extended periods, punctuated by two separate episodes of raptor predations that resulted in multiple mortalities (Figures 3 and 4). This is in contrast to the temporal pattern of raptor predations following traditional releases, when at least 23% of all released parrots were lost to raptors during the first 27 weeks post-release [17], p. 22. Following traditional releases, raptor predations occurred concomitantly with the exodus of individual parrots from the release group and area, and the dispersing individuals were also the predominant victims of predation [17,20]. This is consistent with a predator-driven Allee effect increasing per capita predation risk with decreasing group size. Angulo et al. [34] also reported a similar predator-driven component Allee

effect related to population size in reintroduced island foxes (*Urocyon littoralis*). In that study [34], larger group sizes resulted in lower per capita predation risk from Golden eagles (*Aguila chrysaetos*). Indeed, Llerandi-Román et al. [23] reported that survival of subsequent establishment releases of captive-reared Puerto Rican parrots increased annually following an initial soft release type B at RAF, and attributed this to a steadily increasing group size of resident survivors. During the RAF reintroduction, there were survival benefits that accrued to successive release cohorts due to cultural transmission of acquired survival skills by survivors of previous releases. Similarly, the initial 3-month survival (95%) of the third (2017) soft release type A in EYNF was also higher than that of the previous two such releases, as parrots were also released into a larger group of resident survivors of previous cohorts.

Although attaining adequate survival is paramount in any reintroduction, how surviving individuals distribute themselves within the release landscape is likewise critical, especially in the case of social species. Accordingly, we were encouraged by the comparatively high site fidelity exhibited by parrots released during both the type A and type B releases (Figure 6). Site fidelity not only promotes increased social interactions among individuals of a given cohort, but also—in conjunction with high survival—promotes increased survival and integration of subsequent release cohorts [4,23]. Conversely, low site fidelity can result in greater post-release mortality of individuals dispersing into areas with few, if any, conspecifics, and attendant increased per capita predation risk [17,20], as occurred following traditional and precision releases. This “dilution” and reduction in release group size via low site fidelity can contribute directly to initial Allee effects [9,12,14,16]. In the case of the Puerto Rican parrot, the presence of conspecifics held on-site following releases of individual cohorts likely aided in reducing excessive or premature dispersal. For example, for both the type A and type B releases, we believe that our technique of releasing only one member (male) of potential breeding pairs in a partial cohort release, followed by a second release soon after consisting of the other members of the cohort (including females of pairs), further promoted site fidelity. Because Puerto Rican parrots—like most psittacines—form lifelong monogamous pairs, the strength of this bond may be harnessed in order to retain initially released individuals on-site long enough for them to locate supplemental feeders and begin the adaptation process to the release area. In all such cases, we observed males initially released visiting their mates still held in the release cage, and even attempting to feed them through the cage sides and roof. Upon later release, the other members of the cohort immediately integrated into the previously released group. Moreover, in the case of release type B, we believe the presence of over 250 conspecifics held in captivity at the release site constituted yet another significant factor that aided in promoting site fidelity (Table 1) via increased conspecific attraction (see also [4,5,28]). The long-term presence of on-site supplemental feeders following soft releases type A and type B was also a likely factor in maintaining site fidelity, as also reported by Brightsmith et al. [4] and White et al. [2]. The continual presence of supplemental food sources not only promoted fidelity to the release area, but also greatly aided in monitoring the behaviors and fates of parrots post-release (Figure 7).



Figure 7. A group of captive-reared Puerto Rican parrots converging at a post-release supplemental feeder during March 2016. These parrots had been released nine months earlier (June 2015) during a soft release type A in the El Yunque National Forest of Puerto Rico. Photograph taken by Dailos Hernández-Brito.

Closely related to site fidelity was flock cohesion. For both the soft release type A and type B releases, post-release social cohesion and interactions of released cohorts was extremely high (Table 1, Figure 6), in contrast to traditional and precision releases, in which group cohesion was markedly low. The use of larger and mixed-age release cohorts, combined with long-term supplemental feeding, were the most probable reasons for these findings. The presence of on-site supplemental feeders facilitated daily social interactions by released parrots (Figure 7), which strengthened post-release social bonds and attendant group cohesion, as also reported by Brightsmith et al. [4]. Indeed, the lowest flock cohesion occurred with precision releases (Table 1, Figure 6), in which we released only two individuals during any given release event, and with no post-release support. Moreover, parrots released during precision releases were also released into a very small and low-density wild population, with attendant low conspecific attraction.

Among the parameters recognized as indicative of success in psittacine reintroductions, there are two—survival and subsequent reproduction—that are the most characteristic metrics of success [2]. Of the four types of captive releases of Puerto Rican parrots, only soft releases type A and type B resulted in prompt successful reproduction by released birds (Table 1, Figures 5 and 6). Indeed, in the case of EYNF soft release type B, the successful nesting by two pairs of captive-reared parrots within two months of release—in only 30 days in one case—was unprecedented (Figure 4). Reasons for the more rapid reproduction most likely relate to increased social interactions of all parrots, both released and captive, resulting from larger group sizes associated with type B releases. Importantly, the higher early post-release survival following type B releases also maximized the number of potential breeding individuals during the ensuing reproductive season (Figures 4 and 5), thereby increasing the likelihood of spatial anchoring and establishment of the incipient population. Increased pair formation and breeding efforts in response to larger group sizes have been similarly documented in several social species, including Royal penguins (*Eudyptes schlegeli*) [35], African wild dogs [14], Kakapo (*Strigops habroptila*) [15], and Flamingos (*Phoenicopterus* spp.) [36]. Indeed, for many such species there appears to be a critical

group size threshold, below which social interactions such as pair formation and reproduction are disrupted or inhibited by component Allee effects [17,36,37]. In the case of the Puerto Rican parrot, White et al. [17] hypothesized such a flock size threshold, and believed it to be at least >50 individuals, based on past breeding performance of both wild and captive-released populations. For example, although the number of nesting pairs in the small relict population in EYNF had never exceeded six pairs/year in over 50 years, the breeding population reintroduced at RAF consisted of ten pairs within only six years of initial release [17]. However, since the 1960s, the relict population in EYNF had also never exceeded 50 individuals [17,18] until shortly before hurricane Maria in 2017, when it briefly reached 53–56 individuals (USFWS, unpublished data). In contrast, at RAF the combined presence of both the released and captive parrots resulted in an “effective social population” of 150–200 birds during the critical establishment phase of the reintroduction [17]. Following the initial establishment releases, the RAF wild population—and number of breeding pairs—increased rapidly [17,23]. Similarly, for the soft release type B at EYNF, this “effective social population” approached 300 individuals, and the celerity of pair-formation and post-release reproduction was unprecedented. Thus, in both cases (RAF, EYNF), we hypothesize that soft release type B surpassed a species-specific social threshold and demographic Allee effect inherent to the smaller populations associated with both the traditional and precision releases.

5. Conclusions

Our findings highlight the importance of developing effective strategies for achieving high survival, site fidelity, flock cohesion and prompt reproduction during psittacine reintroductions. Maximizing these parameters may aid in reducing the inherent vulnerability of such reintroductions to potential Allee effects, as described by Deredec and Courchamp [9] and recommended by Armstrong and Wittmer [16].

Consequently, we highly recommend use of soft release type A and B strategies, appropriately adapted to local and species-specific conditions and requirements. For captive-reared Puerto Rican parrots, these strategies have resulted in higher post-release survival, site fidelity and flock cohesion than either the traditional or precision releases. Most importantly, type A and B releases were the only methods that also resulted in prompt post-release reproduction by released parrots (Figures 5 and 6), and associated establishment of a resident breeding population. For those reintroductions in which a substantial numbers of conspecifics are available to be held on-site both before and after any initial releases, soft release type B would be the favored strategy—particularly if releases of reproductive-age individuals can occur shortly before or at the onset of the species reproductive season (sensu Figure 4). Examples include reintroductions at existing captive-rearing or rehabilitation facilities, or the a priori establishment of small captive populations of conspecifics on-site at proposed reintroduction locations [38]. Nevertheless, we recognize that for many reintroduction efforts, the required resources—both biological and financial—may be insufficient to effectively employ this particular strategy. In such cases, a potentially viable option would be the soft release type A strategy. Regardless of the specific strategy employed, diligent efforts directed at minimizing potential Allee effects should be incorporated into the overall reintroduction plan. For psittacines, we believe that both of our recent release strategies (types A, B) have clearly demonstrated the potential to achieve this critical reintroduction goal.

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